MODELING SPATIAL USE PATTERNS OF WHITE-TAILED DEER IN THE FLORIDA EVERGLADES

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
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To Glen--my husband, my soulmate, my lifemate--
for his ability to help me see the 'big picture'
and his unending encouragement and love.

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August 2000

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Cochair: Dr. Kenneth M. Portier
Major Department: Wildlife Ecology and Conservation

As reliance on ecological simulation models increases, proper tools to facilitate their calibration and to increase their reliability become more important. Computer simulations enable scientists to model the effects of environmental catastrophes or management strategies on target populations without conducting expensive or difficult field experiments.

Fractional factorial experiments and response surface methods are presented as design and analysis tools to optimize a simulation model with respect to competing algorithms and parameter values. Issues involving simulation "burn-in" time, the number of iterations required for a simulation to reach a steady-state, and its estimation are discussed. Use of discrepancy functions as quantitative measures of model fit and parameter estimation are examined. Predictive p-values are presented as a tool for

evaluation of the performance of a simulation model, relative to observed field data. Finally, these tools are integrated into an iterative approach for development of simulation models.

An individual-based, spatially explicit (IBSE) simulation model of adult white-tailed deer (*Odocoileus virginianus seminolus*) movement patterns in the wet prairie/hardwood tree island habitat of the Florida Everglades illustrates the use of these techniques. Radio-telemetry data obtained from white-tailed deer on the boundary between Big Cypress National Preserve and Everglades National Park during three normal-to-dry years (1989-92) were used to develop and calibrate the IBSE simulation model. Radio-location data from this same population of deer collected just prior to and during a severe flood (1993-95) were used to validate this simulation. The simulation model can help predict impacts of changes in water management strategies and the impacts of floods and hurricanes on white-tailed deer in the Florida Everglades.

CHAPTER 1
INTRODUCTION

The Florida Everglades is home to a diverse mixture of temperate and sub-tropical flora and a broad collection of fauna, including the Florida panther (*Puma concolor coryi*), the American alligator (*Alligator mississipiensis*), many species of wading birds, and the white-tailed deer (*Odocoileus virginianus seminolus*). The Everglades serves as an example of how anthropogenic activities can drastically change the appearance and function of an ecosystem. National attention was focused on the Everglades when Douglas (1947) described its natural and cultural history in her book, *The Everglades: River of Grass*, and when the Everglades National Park was established that same year. Since then, many scientists have focused their research on understanding the effects of the human-induced changes on this ecosystem and on finding ways to slow or reverse degradation of this unique ecosystem.

White-tailed deer are an ecologically, culturally, and economically valuable wildlife resource throughout the United States (Langenau et al. 1984). White-tailed deer play an important role in the Everglades ecosystem, serving as the major prey of the endangered Florida panther (Maehr et al. 1990) and the bobcat (*Lynx rufus*) (Maehr and Brady 1986). These deer are non-migratory (Loveless 1959b) and exhibit extreme site fidelity, even under adverse environmental conditions (MacDonald 1997, Labisky et al. 1999). The cyclic rising and falling of water levels in this marginal habitat influences

spatial movements (Sargent and Labisky 1995, Zultowsky 1992), habitat use (Hunter 1990, Miller 1993) and reproductive phenology (Loveless 1959b, Richter and Labisky 1985, Boulay 1992).

Historically, the primary goal of deer managers was that of increasing herd productivity and health. Today, throughout much of the United States, managers have the task of controlling deer populations because inflated densities are exerting negative impacts on the landscape. However, in the Everglades, where white-tailed deer maintain low-density populations, managers must insure that deer populations persist. Thus, the maintenance of this deer population is one of the many goals of the large multi-agency research and restoration effort currently in progress in the Florida Everglades (Fleming et al. 1994, USGS 1997, DeAngelis et al. 1998). Part of this restoration effort is the development of the suite of simulation models, Across Trophic Level System Simulation (ATLSS), to predict and compare the effects of alternative hydrologic scenarios on this ecosystem. This suite of models, covering approximately 2.6 million ha, includes physical models (landscape hydrology and topography), process models (e.g., macro- and meso-invertebrates and vegetation), size-structured population models (e.g., fish and amphibians), and individual-based models (e.g., wading birds, white-tailed deer, and Florida panthers) designed to work interactively.

In this dissertation, I explored movement patterns of white-tailed deer in the wet prairie/tree island habitat of the Florida Everglades. An individual-based spatially explicit (IBSE) simulation model was developed to simulate their movement patterns under normal and high water conditions. This model was designed to predict changes in the

movement patterns of the deer population under extreme flood conditions and alternative water management scenarios.

1.1. Simulation Models as Research Tools

Simulation models are important tools in wildlife ecology and conservation, and their use is increasing continuously. Computer simulations enable scientists to model the effects of environmental catastrophes or management strategies on target populations without conducting expensive or difficult field experiments. Early population simulation models ranged from simple growth models, such as logistic growth (Pearl and Reed 1920, Renshaw 1990) to stage- or age-based matrix models (Leslie 1945, Lefkovitch 1965). More recent population models incorporated a spatial component, such as spatial dispersion models (Skellam 1951) and metapopulation models (Levins 1969, Hanski and Gilpin 1996). In the continuing evolution of simulation models, individual-based models, those using individuals as the basic unit (DeAngelis and Gross 1992, Grimm 1999), are the current state of the art. Within this large class of models, IBSE models are used to simulate individual movement processes and interactions over a heterogeneous landscape. This ability to model interactions among individuals and interactions between individuals and their environment provides insight into many ecological processes (Huston et al. 1988, Ims 1995). Furthermore, these models are used to make or defend management decisions (DeAngelis and Gross 1992, Bart 1995, Conroy et al. 1995, Dunning et al. 1995, Turner et al. 1995). As computing power and speed increase and computer costs decrease, more complex IBSE models become feasible.

In individual-based simulations, in which each individual in a population is monitored, stochastic decision rules are developed to control the behavior and choices of

each individual. These models are particularly advantageous when studying populations with few individuals as well as when the study of individual behavior is important. Spatially explicit models allow simulation over a heterogenous environment, making it possible to define spatial relationships among habitat patches and other landscape features such as boundaries and corridors; therefore, the effect of a heterogenous environment on the organism of interest can be investigated. Saaremaa et al. (1988: 125) described the advantages of models using artificial intelligence as "(a) studying population processes based on individual levels of behavior, (b) modeling spatial heterogeneity, (c) building event-driven models, (d) providing a conceptual clarity to model construction, (e) and providing a structure equally well suited to simulating resource management." Intertwining animal movement dynamics and spatial patterns to reveal the larger picture can be accomplished with simulation models. Furthermore, these models comply with two basic doctrines of biology: that individual organisms are represented rather than being combined and represented by one variable (i.e., population size), and that these models distinguish among the locations of individuals (Huston et al. 1988).

Early simulation models of individual animal movements were developed using random walks and correlated random walks (Rolfe and Davenport 1969, Siniff and Jessen 1969, Holgate 1971, Bovet and Benhamou 1988). Effects of communication between individuals on movement patterns also have been explored. Montgomery (1974) expanded Siniff and Jessen's (1969) model to include the impact of communication (i.e., tactile, visual, scent, and vocal) among red fox (*Vulpes vulpes*) dyads on home range formation. Lewis and Murray (1993) modeled territory formation and location of wolf

(*Canus lupus*) packs as a function of scent marks left by neighboring packs and deer densities in the area.

Recently, simulation models have been used to explore the effects of spatial heterogeneity on the dynamics and movements of animals. Effects of various timber harvesting schemes on Bachman's sparrow (*Aimophila aestivalis*) populations in the southeastern U.S. were simulated and evaluated (Pulliam et al. 1992, Liu 1993, Liu et al.1995). A model developed for the California spotted owl (*Strix occidentalis caurina*) explored the effects of habitat connectivity, quality, and quantity on population dynamics (Verner et al. 1992). Turner et al. (1994) developed a model to explore movements of ungulates in Yellowstone National Park in response to fire. Riesenhoover et al. (1997) designed a simulation model to predict impacts of alternative deer management strategies on a population. Cramer (1999) developed an IBSE model to predict movements of Florida panthers in north Florida, should a reintroduction program be enacted. Although these simulations are predictive and often are not fully validated, they may still aid in understanding the dynamics of species and landscape interactions.

The increasing reliance of management decisions on simulation models drives the necessity to develop tools to adequately calibrate and validate these models. Most individual-based models incorporate a large number of parameters (Grimm 1999). Some model parameters, such as number of offspring or survival rate, are estimated from published values. In contrast, parameters characterizing movement patterns of individuals in a simulation rarely can be estimated from published values or even derived from measurable variables on study animals. These parameters (e.g., distance an individual can 'see' when making a movement decision or the effect of previous movements on the

current movement decision) are either difficult or impossible to estimate from field data. However, the best-fitting movement algorithms and associated parameter values can be determined by evaluating discrepancies in measurable outcomes (e.g., home range size) between study animals and simulated animals.

Bart (1995) and Conroy et al. (1995) suggested guidelines for model development and testing that included the need for clearly stated model objectives, a description of the model structure, and a sensitivity analysis to assess effects of parameter uncertainty on model outputs. In addition, model development also requires verification, calibration, and validation. As defined by Rykiel (1996), verification is a demonstration that the model form is correct, calibration is the estimation and adjustment of model parameters to improve agreement between model output and observed data, and validation is a demonstration that a model possesses the accuracy required for its intended applications.

Although individual-based models ought to be more testable than state-variable models (Murdoch et al. 1992), only 36% (18 of 50) of the individual-based modeling papers reviewed by Grimm (1999) explicitly discussed validation or corroboration of the presented models. Statistical tools for validation of simulation models have been developed primarily in two fields of research: ecological process and population models (e.g., Van der Molen and Pintér 1993, Rykiel 1996) and operations research and industrial engineering settings (e.g., Sargent 1984, Kleijnen 1987).

1.2. Objectives

The main objective of this dissertation was to develop an IBSE simulation model of movement patterns of adult white-tailed deer in the Florida Everglades. The model provides a means of exploring patterns of spatial use of deer in response to environmental

catastrophes (e.g., tropical storms) and to different management regimes (e.g., water control). Furthermore, the statistical methodologies used to calibrate and validate this IBSE model provide a foundation for the development of future simulation models.

The specific objective of the simulation model was to predict how temporal landscape changes (i.e., rising and falling water levels) affect movement patterns of deer in the Florida Everglades. The simulation model was calibrated with radio-telemetry data collected from 1989 to 1992 under dry-to-normal hydrological conditions. The same simulation model also was run under flood conditions, like those experienced during the flood that began in the fall of 1994, to evaluate the changes in movement patterns during an environmental catastrophe. In the development stages of this model, several calibration issues were addressed: (1) development of an approach to test the IBSE model relative to observed data with the use of discrepancy measures, (2) development of an effective approach for calibrating an IBSE model with sequential experimentation, and (3) evaluation of the predictive abilities of an IBSE simulation with predictive p-values. The model was validated with radio-telemetry data collected just prior to and during the flood of 1994-95.

1.3. Dissertation Structure

In Chapter 2, the Everglades ecosystem and the study area are described. In Chapter 3, the white-tailed deer calibration data are discussed in detail. The statistical techniques employed to calibrate the IBSE model and details of the final model are discussed in Chapter 4. In Chapter 5, the white-tailed deer validation data are presented and in Chapter 6, details of model validation are discussed. Conclusions and implications of the simulation results are discussed in Chapter 7.

CHAPTER 2
EVERGLADES ECOSYSTEM AND THE STUDY AREA

Understanding the ecosystem under consideration is essential prior to simulation development. In this chapter, the Everglades ecosystem and the study area are discussed. Development of the temporal-spatial hydrology map is described.

2.1. The Everglades Ecosystem

2.1.1. Climate and Topography

The Everglades ecosystem is characterized by a subtropical climate with alternating dry winters (November-April) and wet summers (May-October). Mean monthly temperature ranges from 14 C in January to 28 C in August. Mean annual precipitation is 136 cm, two-thirds of which falls between May and October (Duever et al. 1986). The onset, duration, and intensity of the wet seasons are highly variable; thus, periods of either drought or flooding occur. Tropical cyclones (hurricanes and tropical storms) occur in this region of Florida at a rate of one every 3 years (Gentry 1984), and often exacerbate the severity of floods. Frost occurs infrequently, and a severe freeze occurs at a rate of one every 10 years (Drew and Schomer 1984).

The Everglades region is nearly flat, with an overall gradient on the order of 2 cm/km in a north-south direction with steeper gradients at smaller spatial scales (Gunderson 1994), and is characterized by a southwestward sheet flow of water (Duever

et al. 1986). The range of elevations between the lowest and highest vegetation communities is approximately 1.5 m (Gunderson 1994).

2.1.2. Flooding and Water Control

The historic Everglades, a 3.6 million ha mosaic of marsh, slough, tree islands, and pinelands, extended from central Florida (Kissimmee Chain of Lakes) southward to the Florida Bay. "Replumbing" of the Everglades watershed began with the Swamplands Act of 1850, which authorized the transfer of 8.1 million ha of the Everglades to the state of Florida for the purpose of drainage and reclamation. In the 1880s, a millionaire entrepreneur purchased and drained more than 20,000 ha in the Kissimmee basin and built the first canals through the Everglades, demonstrating that the land was very productive and could be lucrative for agriculture (Blake 1980). To control the impacts of devastating floods and hurricanes on human populations and to further agricultural production, drainage of the Everglades and flood control measures on Lake Okeechobee continued into the early 1900s. The Central and Southern Flood Control District, later renamed the South Florida Water Management District (SFWMD), was formed in 1949, consolidating water management functions into one entity. Between 1950 and 1973, the SFWMD and the Army Corps of Engineers constructed a network of canals, pumps, and other water control structures. In the northern Everglades, the Water Conservation Areas were created to hold water away from the populated coastal areas and retain it for agricultural and municipal needs (Light and Dineen 1994). During periods of high rainfall, overflows from these areas were released southward often creating artificially high water levels in the Everglades National Park and surrounding protected areas.

Approximately half of the original Everglades ecosystem remains today (Davis and Odgen 1994), but, in many places, the hydrologic regimes bear little resemblance to the historic predrainage flows (Light and Dineen 1994). Hydrology is the most important force shaping the Everglades, and it is the force that was most altered and has most affected the remaining system (Brandt 1997). Water control measures have exacerbated the effects of floods and droughts in the remaining natural system, and changes in hydroperiod length and intensity have altered vegetative communities. Modifications in hydrologic patterns have contributed to changes in plant communities, changes and decreases in wildlife populations, and changes in the historic functioning of the Everglades (Loveless 1959a, Alexander and Crook 1984, Davis et al. 1994, Odgen 1994).

2.2. Study Area

The 30,000 ha study area (Fig. 2.1) is located in the wet prairie/tree island ecosystem that extends from the Stairsteps Unit of the Big Cypress National Preserve (BCNP) south into Everglades National Park (ENP). It is bounded on the north by Loop Road, on the west by Lostmans and Dayhoff Sloughs, and on the east and south by Shark River Slough. The habitat map (Fig. 2.2) was developed by Miller (1993); it depicts ten habitats (Table 2.1), using 20-m x 20-m pixels (referred to as "20-m pixels") with an estimated accuracy of 80.4%. Miller (1993) discussed the details of development of this map and its accuracy evaluation.

2.2.1. Vegetation Classification and Hydroperiod Length

Soil depth and type, hydroperiod (length of annual inundation), and fire are the primary factors in the development of plant occurrences in the wet prairie habitat of the Everglades (Duever 1984). Various vegetation classifications of the Everglades region are

reported in the literature (see Olmsted and Armentano [1997] for summary). The vegetation classification scheme used in this study follows the broad classifications of Duever (1984): forested uplands, non-forested wetlands, and forested wetlands.

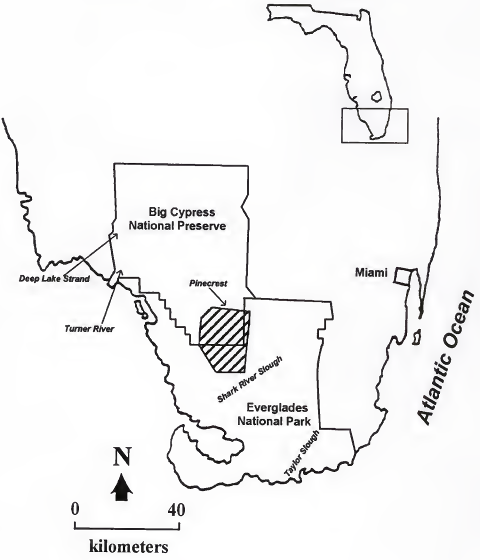

Figure 2.1. Location of study area within Big Cypress National Preserve (BCNP) and Everglades National Park (ENP), Florida. The study area is marked by the hashed lines.

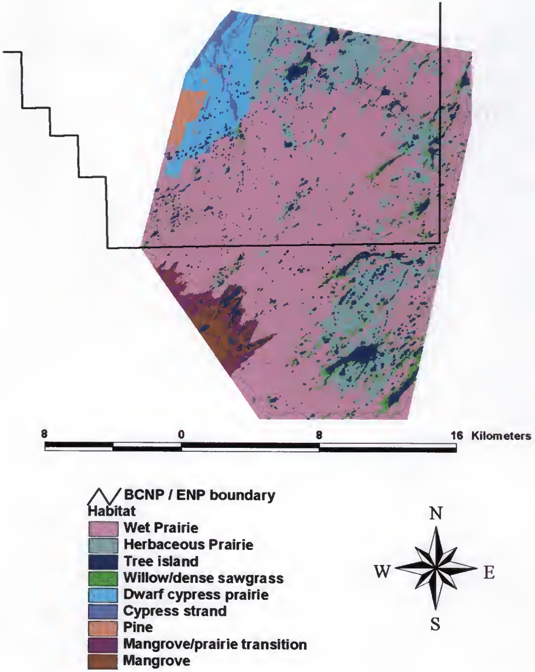

Figure 2.2. Habitat within the study area of BCNP and ENP, Florida. Map developed by Miller (1993).

Table 2.1. Areal coverage of the habitats in the study area, BCNP and ENP, Florida [after Miller (1993)].

Habitat	Area (ha)	(%)
Wet prairie	21758	62.9
Herbaceous prairie	5001	14.5
Tree islands	2201	6.4
Willow/dense sawgrass	1469	4.2
Dwarf cypress prairie	2045	5.9
Cypress strand	399	1.2
Pine	143	0.4
Pine with dwarf cypress	248	0.7
Mangrove/prairie transition	568	1.6
Mangrove	735	2.2

2.2.1.a. Forested uplands

Hardwood tree islands, including hardwood hammocks and bayheads, account for approximately 6.4% of the study area (Miller 1993). Many of these tree islands are characterized by an elongated shape, as formed by the flow of surface water, although some in the drier prairies have a more rounded shape. Size of tree islands in the study area is variable (0.04-208 ha), but most (83%) are <1 ha (Fig. 2.3). Tree islands have a closed dome canopy of 6-20 m high.

Hardwood hammocks are elevated above the surrounding prairie ≥ 1 m, often on a bedrock outcrop (Craighead 1984). Hammocks are composed primarily of flood intolerant species including live oak (*Quercus virginiana*), wild tamarind (*Lysiloma latisiliqua*), gumbo limbo (*Bursera simaruba*), and strangler fig (*Ficus aurea*) (Duever et al. 1986). Bayheads are elevated above the surrounding prairie, but less so than hardwood hammocks, and are composed of flood tolerant temperate and tropical hardwoods

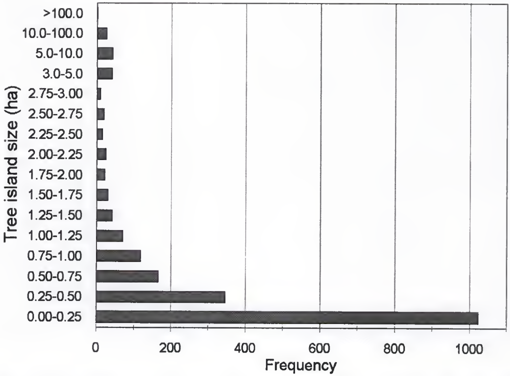

Figure 2.3. Histogram of size of tree islands in the study area. Note that not all the widths of size categories for tree islands are the same.

including red bay (*Persea borbonia*), wax myrtle (*Myrica cerifera*), cocoplum (*Chrysobalanus icaco*), and dalhoon holly (*Ilex cassine*). Common ground cover in tree islands includes royal fern (*Osmunda regalis*), swamp fern (*Blechnum serrulatum*), bloodberry (*Rivina humilis*), and greenbriar (*Smilax* spp.) (Duever et al. 1986).

Inundation of hardwood hammocks is rare; however, partial inundation of bayheads is frequent. Between 1953 and 1978, the hardwood hammocks in the Pinecrest region of Big Cypress National Preserve were estimated to have been inundated only 2 days (Gunderson and Loope 1982a). Schomer and Drew (1982) estimated a hydroperiod length of <1 month in hardwood hammocks. Shallow inundations lasting 0.3-1.5 months in hardwood hammocks and bayheads in BCNP were reported by Duever et al. (1986).

Slash pine (*Pinus elliottii* var. *densa*) forests are restricted to the extreme western edge of the study area. Pine forests have a grassy understory, commonly *Muhlenbergia* spp. and *Andropogon* spp.; drier forests often have a saw palmetto (*Serenoa repens*) understory (Duever et al. 1986). Hydoperiods are often non-existent, but if present, they average <2 months in length (Duever et al. 1986, Olmsted et al. 1980).

2.2.1.b. Non-forested wetlands

Non-forested wetlands, principally sparse sawgrass (*Cladium jamaicensis*) marshes and muhly grass (*Muhlenbergia filipes*) prairies, comprise 77.4% of the study area (Miller 1993). Sparse sawgrass marshes, which comprise 62.9% of the study area, are dominated by sawgrass, but also contain maidencane *(Panicum hemitomon)*, spikerush (*Eleocharis* spp), muhly grass, as well as other grasses, sedges, and rushes (Duever et al. 1986). Patches of pickerelweed (*Pontederia* spp.) and arrowhead (*Sagittaria* spp.) are found in slight depressions in the marsh. Muhly grass prairies, also termed 'herbaceous prairies', constitute 14.5% of the study area and occur at slightly higher elevations than sparse sawgrass marshes (Miller 1993). These prairies support a higher diversity of herbaceous forbs and grasses, sedges, and rushes than sparse sawgrass marshes.

Estimates of hydroperiod length in sparse sawgrass marshes and muhly grass prairie vary depending on geographic location and habitat classification. Annual hydroperiod estimates for sparse sawgrass in Shark Slough ranged from 6-12 months between 1953-1980 (Olmsted and Armentano 1997) and from 2.2-7.6 months in Taylor Slough between 1961-1977 (Olmsted et al. 1980). Annual hydroperiod estimates for muhly grass prairie ranged from 1.0-4.9 months in Taylor Slough between 1961-1977

(Olmsted et al. 1980), from 0.0-6.7 months in the Turner River area between 1964-1978 (Gunderson et al. 1982), and from 1.0-3.6 months in Deep Lake Strand between 1973-1980 (Gunderson and Loope 1982b). Duever et al. (1986) defined wet prairies in BCNP to have hydroperiods of 1.7-5.0 months and freshwater marshes to have hydroperiods of 7.5-9.0 months. Kushlan (1990) defined wet prairies to have hydroperiods of <6 months and sawgrass marshes to have hydroperiods of 6-9 months.

2.2.1.c. Forested wetlands

Willow (*Salix caroliniana*) forms dense thickets in flowing water sites, often surrounding tree islands and forming "tails" following the direction of water flow. Stands of tall (1-3 m) dense sawgrass are frequently found in association with willow thickets. These tall dense sawgrass strands frequently occur at slightly higher elevations than the surrounding prairie, and exhibit a reduced hydroperiod (Kushlan 1990). However, Olmsted and Armentano (1997) noted that east and west of Shark Slough, tall sawgrass strands are often found at lower elevations than the surrounding sparse sawgrass or spikerush marsh and exhibit hydroperiods of 6-8 months. In southern Taylor Slough, a willow/sawgrass stand had an estimated hydroperiod of 9.0-10.3 months between 1961-1977 (Olmsted et al. 1980).

Cypress domes and strands (*Taxodium* spp.), which are restricted to the northwestern portion of the study area, occur in circular or elongated depressions in the bedrock and are characterized by an understory of herbaceous and woody species, such as bladderwort (*Utricularia* spp.), swamp fern (*Blechnum serrulatum*), buttonbush (*Cephalanthus occidentalis*) and willow (*Salix caroliniana*). Hydroperiods in cypress strands and domes average 8.3-9.7 months (Duever et al. 1984). Dwarf cypress forest is

an open forest with stunted, widely spaced cypress tress and a herbaceous understory. Hydroperiods in dwarf cypress forests range from 4-12 months (Flohrschutz 1978, Gunderson and Loope 1982a).

Red mangrove (*Rhizophora mangle*) forests are restricted to the southwestern edge of the study area. These tidally submerged woodlands occur along the coast and inland along coastal rivers (Scholl 1968). Water in these swamps is <60 cm deep; and many interior areas are not inundated during an average high tide. The swamp floor is submerged entirely during extreme high tides, and many areas are exposed subaerially during low tide.

2.2.2. Hydrology Patterns

Hydrology patterns were inferred using historical data from hydrologic station P-34, which was located centrally in the study site in an area characterized as wet prairie or sparse sawgrass marsh (Fig. 2.4). During the period of record (1953-1995), data were missing for the following 4 months: October 1980, May 1991, January 1993, and February 1993. These missing data were estimated with an analysis of covariance, using water depths from a neighboring water gauge as the covariate. Three water gauges were identified as potential covariates (Fig. 2.4). NP-205, located 13 km northeast of P-34 in a drier prairie, had water levels strongly correlated with levels at P-34 ($r=0.876$, $n=251$); however, the period of record did not start until October 1974, and data were not available for January 1993 and February 1993. P-35 was located 18 km south of P-34 in southern Shark Slough; however, the correlation between water depths was not as strong ($r=0.675$, $n=511$). Measurement of water depths at P-36, located 17 km southeast of P-34

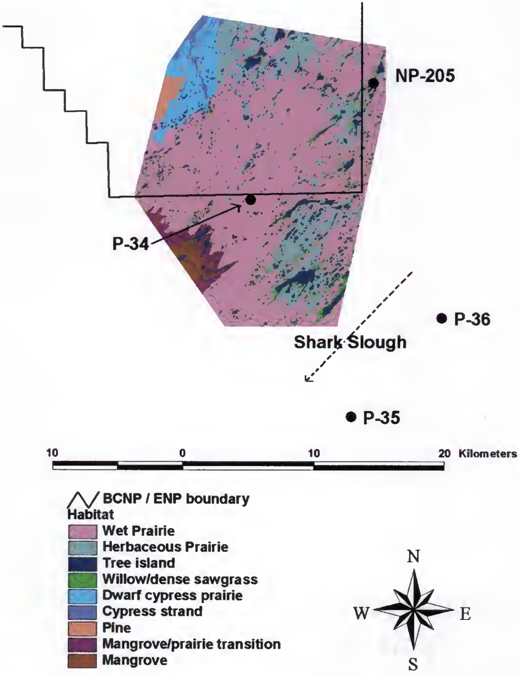

Figure 2.4. Study area with locations of neighboring hydrologic gauges, P-34, NP-205, P-35, and P-36.

in central Shark Slough, began in February 1968 and the correlation with water depths at P-34 was the strongest (r=0.904, n=331).

Based on the quantity of available data and strength of correlation, P-36 was chosen to predict water depths during the 4 missing months. The model included water depth at P-36 as a quantitative covariate with year and month included as qualitative factors. The inclusion of year and month improved the model fit (adjusted R^2=0.817 for model with P-36 and adjusted R^2=0.888 for model with P-36, year, and month). Other models that accounted for the temporal correlation of the data and the cyclical nature of the water depths were fit to the data. However, these models did not provide improved fit, possibly because of the intrinsic random nature of rainfall patterns and changes in water control measures during the period of record.

Relative to four other gauging stations in wetland communities in ENP, P-34 had the lowest water levels and the shortest period of annual inundation; however, it also had the largest range of water level fluctuations (Gunderson 1990). Between 1954-1985, hydroperiods ranged from 2-12 months with a historical mean of 6.6 months. No differences in hydropattern among community types were detected because of high year-to-year variability.

From 1989 to 1992 (during the first field study), wet seasons appeared typical; however, dry seasons were much drier than average (Figs. 2.5 and 2.6). Hurricane Andrew, a relatively dry hurricane, moved through the study area in August 1992 and caused extensive damage to the tree islands by blowing down and completely defoliating most trees in its path (Labisky et al. 1999). The second field study was conducted from 1993 to 1995. The fall of 1994 was extremely wet, with >100 cm of rain occurring

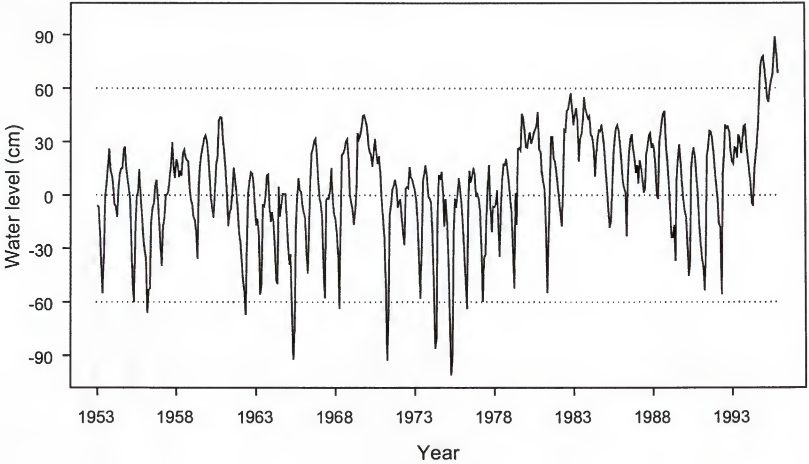

Figure 2.5. Mean monthly water levels recorded at P-34 hydrologic station, Everglades National Park, Florida, January 1953-December 1995. Depths were predicted for October 1980, May 1991, January 1993, and February 1993.

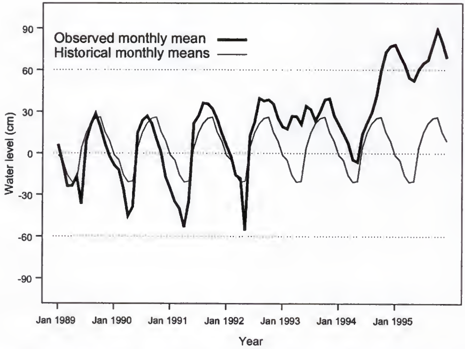

Figure 2.6. Mean monthly water levels recorded at P-34 hydrologic station from January 1989 to December 1995 and historical monthly means from 1953-1985. Depths were predicted for May 1991, January 1993, and February 1993.

between August and November, culminating with Tropical Storm Gordon in November 1994 which contributed >20 cm of rain. Water levels remained high in the study area throughout 1995.

A relative elevation map was created to simulate changes in water depths over time. Elevation of each habitat, relative to P-34, was derived from a literature review and estimation of annual hydroperiod length for various elevations (Table 2.2). The 20-m pixel elevation map was created from the habitat map and the estimated elevations (Fig. 2.7). To allow for gradual changes in elevation on habitat edges, nearest-neighbor averaging was performed on the elevation map.

Table 2.2. Estimated elevation of each habitat, relative to P-34 hydrologic station[a], and estimated minimum, median, and maximum hydroperiod lengths (months per year) for each habitat.

Habitat	Estimated elevation relative to P-34 (cm)	Estimated hydroperiod 1953-1995		
		min	med	max
Wet prairie	0	2	7	12
Herbaceous prairie	20	0	3	12
Tree islands	80	0	0	2
Willow/dense sawgrass	-15	5	9	12
Dwarf cypress prairie	5	0	6	12
Cypress strand	-10	5	9	12
Pine	80	0	0	2
Pine with dwarf cypress	30	0	0	12
Mangrove/prairie transition	-5	3	8	12
Mangrove	-20	6	12	12

[a] P-34 hydrologic station was located in wet prairie habitat (Fig. 2.4).

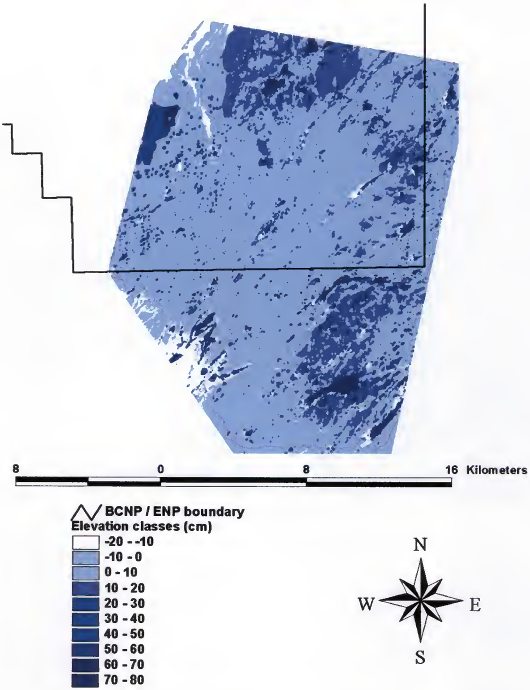

Figure 2.7. Estimated elevation map (relative to P-34 hydrologic station) within the study area.

CHAPTER 3
WHITE-TAILED DEER MODEL CALIBRATION DATA

The white-tailed deer population on the BCNP/ENP study site was the subject of intensive investigation from 1989-1992 (Boulay 1992, Sargent 1992, Zultowsky 1992, Miller 1993, Sargent and Labisky 1995, Labisky et al. 1999). The white-tailed deer data used for model calibration were analyzed to provide a starting point for the development of the simulation model. During the collection of this calibration data, environmental conditions ranged from mild drought to typical (Fig. 3.1). The simulation model developed in Chapter 4 reflects the movement patterns and habitat use dynamics explored in these analysis.

3.1. Data Collection Methods

White-tailed deer were captured exclusively by helicopter-netgunning (Barrett et al. 1982, Labisky et al. 1995). Each captured deer was aged, measured, and marked with a radio-transmitter/collar, equipped with motion-sensitive activity (2X signal pulse) and mortality (4X signal pulse) modes (Wildlife Materials, Inc., Carbondale, IL). Due to the inaccessibility of the study area, all radio-monitoring was conducted during daylight hours from a fixed-wing aircraft. To obtain unbiased temporal monitoring, radio-locations for each deer were evenly distributed among four daylight periods: sunrise to 2 hours post-sunrise, 2 hours post-sunrise to noon, noon to 2 hours pre-sunset, and 2 hours pre-sunset to sunset. By stratifying the radio-locations across the entire day, any diurnal

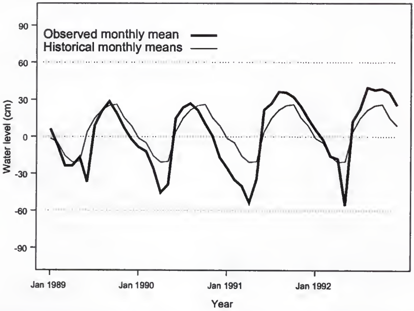

Figure 3.1. Mean monthly water levels recorded at P-34 hydrologic station, and historical monthly means from 1953-1985. Depths were predicted for May 1991.

patterns present in movement characteristics or habitat associations would be equally represented and, thus, not impact annual and hydrologic season summary statistics. Each deer was located, on average, once every 5 days. The location error associated with aerial-based telemetry, estimated from blind placement of dummy radio-collars, was <30 m (Miller 1993).

3.2. Data Summary Methods

A deer was classified as a resident of either BCNP or ENP if ≥75% of its radio-locations were located in one of the management units. Data were summarized on an annual basis with the annual cycle defined to begin on April 1 of the calendar year. This annual cycle was divided into four periods based on reproductive phenology (Labisky et al. 1995). Weaning and pre-rut occur from April through June. Males are in rut and females in estrus from July through September. Post-rut and pregnancy occur from

October through December, coinciding with the peak hunting season in BCNP. Fawning and antlerogenesis occur January through March, and all deer were assigned arbitrary birthdates of April 1. For the calibration data set, data were collected for 3 annual cycles [1989 (1 April 1989-31 March 1990), 1990 (1 April 1990-31 March 1991), and 1991 (1 April 1991-31 March 1992)]. Deer included in an annual cycle were required to have a minimum of 50 radio-locations, be monitored for a minimum of 9 months during that annual cycle, and exhibit no dispersal movements.

Differences in the measured parameters between hydrologic seasons also were estimated. Sufficient data were collected for 5 hydrologic seasons [89DRY (1 November 1989 - 30 April 1990), 90WET (1 May 1990 - 31 October 1990), 90DRY (1 November 1990 - 30 April 1991), 91WET (1 May 1991 - 31 October 1991), and 91DRY (1 November 1991 - 30 April 1992)]. Deer included in these analyses were required to have been monitored for a minimum of 2 sequential hydrologic seasons and exhibit no dispersal movements during those seasons. Each included deer had a minimum of 30 radio-locations and was monitored for a minimum of 5 months in each season. That condition was relaxed in 91DRY to a minimum of 24 radio-locations and 4 months of observation because radio-monitoring ended on 31 March 1992.

3.2.1. Annual Cycles

Annual home range size was calculated using the 95% fixed kernel estimator with least squares cross validation (Silverman 1986, Worton 1989, Seaman and Powell 1996). Distance between centers of annual home ranges was calculated to access the degree of site fidelity. Mean distance between radio-locations for each deer was used as a proxy for the distance that a deer traveled during a 5-day interval. This statistic cannot be used as a

measure of the total distance that a deer traveled over a 5-day interval, but can be used as an indicator of the minimum distance a deer traveled over 5 days. Percentage of radio-locations in each habitat was used to establish habitat selection patterns. Sample means were weighted to account for deer with multiple years of observations.

Resource selection was evaluated using chi-square analyses (Neu et al. 1974, Manly et al. 1993) for sample design II (multiple observations on same individual, assume same habitat availability for all individuals) and sample design III (multiple observations on same individual, estimate habitat availability for each individual) as defined by Thomas and Taylor (1990). To insure deer with multiple years of observation did not unduly influence summary statistics, 1 year of observational data from each deer was randomly selected for inclusion into these analyses. The original study and deer captures focused on tree islands and prairies of the study area; therefore, the few deer spending a large portion of their time in the pine, cypress, and mangroves were not included in these analyses. Separate summary statistics were calculated for females and males.

For the sample design II analyses, habitat availability was assumed equal for all deer. After removing pine, cypress, and mangrove areas from the map, wet prairie, herbaceous prairie, tree islands, and willow/sawgrass accounted for 72%, 16%, 7%, and 5% of the study area, respectively. The notation used for the habitat analyses was:

π_i = known proportion of habitat i in the study area,

u_{ij} = number of observations of the j^{th} animal in the i^{th} habitat,

u_{i+} = total number of observations of all n animals in the i^{th} habitat,

u_{+j} = total number of observations of the j^{th} animal in all habitats, and

u_{++} = total number of observations.

Selection ratios for each habitat were calculated. Each ratio was proportional to the probability of the given habitat being utilized, assuming the individual had unrestricted access to the entire distribution of habitats. The selection ratio and associated variance for each habitat for this population of deer was estimated with

$$\hat{w}_i = \frac{u_{i+}}{\pi_i u_{++}}$$

$$\text{var}\left(\hat{w}_i\right) = \left\{\sum_{j=1}^{n} \frac{\left(\frac{u_{ij}}{\hat{w}_i u_{+j}}\right)^2}{n-1}\right\}\left\{\frac{n}{u_{++}{}^2}\right\}$$

Simultaneous Bonferroni confidence intervals for the selection ratios were calculated using an α-level of 0.05. Those confidence intervals not including 1 indicated either selection for (ratio >1) or against (ratio <1) a particular habitat, and confidence intervals including 1 indicated no evidence of selection for or against a particular habitat. A second sample design II analysis was performed, using the percentage of each habitat contained inside the 100% minimum convex polygon (MCP) home range for each deer, rather than the number of radio-locations in each habitat.

For the sample design III analyses, habitat availability was estimated individually for each deer using the proportions of habitats contained inside the 100% MCP home ranges. Notation was the same as defined above for design II except that π_{ij} was the known proportion of habitat *i* contained in the home range of individual *j*. Population selection ratios and associated variances for each habitat were estimated using

$$\hat{w}_i = \frac{u_{i+}}{\sum_{j=i}^{n} \pi_{ij} u_{+j}}$$

$$\mathrm{var}\left(\hat{w}_i\right) = \frac{\left(\sum_{j=1}^{n} \left(u_{ij} - \hat{w}_i \pi_{ij} u_{+j}\right)^2 \frac{n}{n-1}\right)}{\left(\sum_{j=1}^{n} \pi_{ij} \pi_{+j}\right)^2}$$

Simultaneous Bonferroni confidence intervals for these population selection ratios using an α-level of 0.05 also were calculated.

3.2.2. Hydrologic Seasons

For each deer, home range size for each of the hydrologic seasons was calculated using the 95% fixed kernel estimator with least squares cross validation. Mean distance between radio-locations for each deer served as a proxy for the distance a deer traveled during a 5-day interval. Mean home range size and distance between consecutive radio-locations and their standard errors were estimated using the number of seasons each deer was in the sample population as weights. Differences between the WET and DRY seasons were tested using a mixed model analysis with deer as a random effect and hydrologic season as a fixed effect.

Percentage of radio-locations occurring in each habitat was used to establish differences in seasonal habitat selection. Deer observed in pine, cypress, or mangrove habitats were not included in these analyses. The generalized Cochran-Mantel-Haenszel test (Birch 1965, Agresti 1990) was conducted for each gender to test for an overall association between hydrologic season and habitat selection. Additionally for each

deer, a chi-square test was performed to test the hypothesis that there was a difference in the distribution of radio-locations across habitats between WET and DRY seasons.

3.3. Data Summary

Estimated white-tailed deer densities for 1990-1992 were 3.65 (se=1.47) deer/km^2 for the hunted BCNP population and 4.68 (se=1.00) deer/km^2 for the non-hunted ENP population (Labisky et al. 1995). The data set used for model calibration included yearling and adult deer that were captured, radio-collared, and monitored between 1989 and 1992. Data from 46 yearling or adult deer were used for initial model calibration (Appendix A). Twenty-four deer were radio-monitored for 1 year, 18 deer for 2 years, and 10 deer for 3 years. Ten deer were radio-monitored for 2 hydrologic seasons, 15 deer for 3 seasons,12 deer for 4 seasons, and 6 deer for 5 seasons.

3.3.1. Annual Cycles

The mean annual home range size of females was 271 ha (se=20, n=29), with a range from 90 ha to 600 ha. Male home ranges were slightly larger (316 ha, se=49, n=17) ranging from 102 ha to 1086 ha. Distance between consecutive home range centers was similar for both genders; females had a mean distance of 307 m (se=53, n=17) and males had a mean distance of 243 m (se=56, n=9).

Time intervals between radio-locations ranged from 1 to 14 days; however, many (46%) were 5 days in length. To ensure the length of the measurement interval was not influencing the straight-line distance between locations, an analysis of covariance (ANCOVA) was performed. Distance between consecutive measurements had a skewed distribution (Fig. 3.2) and was log-transformed prior to analysis. In the ANCOVA model, the fixed effects were year (1989, 1990, 1991), days between radio-locations (linear

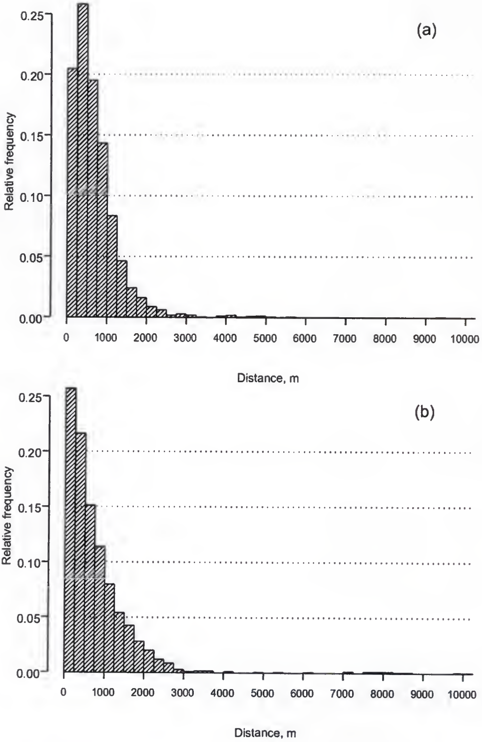

Figure 3.2. Histogram of straight-line distances (m) between consecutive radio-locations for (a) female and (b) male white-tailed deer.

covariate), and their interaction; the random effect was deer. Using an α-level of 0.05, the fixed effects did not have a significant effect on distance between consecutive measurements (Table 3.1). The mean distance between consecutive locations was 686 m (se=29, n=29) for females and 779 m (se=79, n=17) for males. Most distances were <750 m (65%) and nearly all <1500 m (90%), but deer occasionally were recorded traveling longer straight-line distances (maximum observed distance=10240 m).

Table 3.1. Results from the analyses of covariance for log-transformed distance between consecutive radio-locations for female and male white-tailed deer.

Fixed Effect	df numerator	df denominator	p-value
Female			
YEAR	2	3034	0.4366
DAYS	1	3034	0.0766
YEAR*DAYS	2	3034	0.6011
Male			
YEAR	2	1715	0.1924
DAYS	1	1715	0.5992
YEAR*DAYS	2	1715	0.1596

Based on simple summaries of percentage of occurrances in each habitat (Table 3.2), females appeared to select for wet prairie more strongly than males, and males appeared to select for tree islands and willow/dense sawgrass more strongly than females.

Habitat-use patterns were evaluated quantitatively using selection ratios. When evaluating habitat selection based on the choice of a home range (100% MCP), assuming equal availability of habitat for all individuals, females exhibited no significant selection for or against any habitat since all the confidence intervals included 1 (Table 3.3). However, males selected home ranges with less wet prairie and more willow/dense sawgrass than expected, based on availability in the study area (Table 3.3). When the

selection ratios were calculated using radio-locations and assumed equal habitat availability for all individuals, both females and males demonstrated habitat preferences (Table 3.4). Both genders selected against wet prairie, had no selection for or against herbaceous prairie, and selected for tree islands and willow/dense sawgrass; however, males tended to exhibit stronger selection for or against a particular habitat than females, as evidenced by the more extreme selection ratios (i.e., selection ratios farther from 1). These selection ratios were more extreme than those based on selection of home range area (Table 3.3), which was expected because the analysis based on home range areas assumed equal use of all the area contained inside the home range. Similar selection trends were observed when habitat availability was estimated separately for each individual using 100% MCP (Table 3.5). Both females and males selected against wet prairie, selected neither for nor against herbaceous prairie, and selected for tree islands and willow/dense sawgrass inside their home ranges. These results were similar to Miller's (1993) findings.

Table 3.2. Mean percentage of radio-locations in each habitat for the study sample of white-tailed deer in BCNP and ENP, April 1989 to March 1992.

Habitat	Female[a]		Male	
Wet prairie	53	(4)[b]	25	(4)
Herbaceous prairie	17	(3)	20	(3)
Tree islands	17	(2)	33	(4)
Willow / dense sawgrass	9	(1)	18	(2)
Dwarf cypress prairie	1	(1)	2	(2)
Cypress strand	<1	(<1)	1	(1)
Pine	<1	(<1)	<1	(<1)
Mangrove	2	(2)	1	(1)

[a] Sample sizes: female (29), male (17).
[b] Standard error in parentheses.

Table 3.3. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for habitat inside 100% MCP for the study sample of white-tailed deer in BCNP and ENP, April 1989 to March 1992.

Habitat	Female[b]		Male	
Wet prairie	1.05	(0.90, 1.20)	0.77	(0.56, 0.98)
Herbaceous prairie	0.88	(0.08, 1.39)	1.51	(0.94, 2.08)
Tree islands	0.74	(0.35, 1.13)	1.67	(0.68, 2.66)
Willow/dense sawgrass	1.02	(0.58, 1.46)	1.73	(1.13, 2.33)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female (26), male (12).

Table 3.4. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for radio-locations for the study sample of white-tailed deer in BCNP and ENP, April 1989 to March 1992.

Habitat	Female[b]		Male	
Wet prairie	0.75	(0.59, 0.91)	0.35	(0.18, 0.51)
Herbaceous prairie	1.15	(0.60, 1.70)	1.14	(0.88, 1.69)
Tree islands	2.41	(1.47, 3.34)	5.29	(3.64, 6.90)
Willow/dense sawgrass	2.14	(1.53, 2.76)	3.96	(2.95, 4.94)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female (26), male (13).

Table 3.5. Selection ratios and 95% Bonferroni confidence intervals[a] using the design III analysis for the study sample of white-tailed deer in BCNP and ENP, April 1989 to March 1992.

Habitat	Female[b]		Male	
Wet prairie	0.72	(0.62, 0.83)	0.45	(0.30, 0.59)
Herbaceous prairie	1.28	(0.96, 1.60)	0.79	(0.45, 1.12)
Tree islands	3.16	(1.97, 4.35)	3.19	(1.67, 4.71)
Willow/dense sawgrass	2.05	(1.13, 2.97)	2.16	(1.44, 2.89)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female (26), male (12).

3.3.2. Hydrologic Seasons

Mean WET season home range size of females (n=26) was 211 ha (se=17) and was significantly different (p=0.0025) from the mean DRY season home range size of 303 ha (se=36). The mean WET season home range size of males (n=17) was 301 ha (se=48) and was significantly different (p=0.0007) from the mean DRY season home range size of 187 ha (se=36).

Mean distance between consecutive radio-locations followed a pattern similar to home range sizes. Mean distance between consecutive radio-locations in the WET season for females (n=26) was 638 m (se=27) and was significantly different (p=0.0025) from the mean DRY season distance of 722 m (se=34). Mean distance between consecutive radio-locations in the WET season for males (n=17) was 866 m (se=67) and was significantly different (p=0.0007) from the mean DRY season distance of 664 m (se=81).

There was no evidence of a change in habitat use between the hydrologic seasons based on radio-locations for females (Cochran-Mantel-Haenszel test, p=0.75, df=3, n=2702) (Table 3.6). Of the 24 females included in this analysis, only three had a significant association between hydrologic season and habitat (chi-square test, $p<0.05$, df=3), but there was no commonality in the associations between hydrologic season and habitat. There was evidence of a change in the distribution of habitat use based on radio-locations for males (Cochran-Mantel-Haenszel test, p=0.001, df=3, n=1498) (Table 3.6). During the DRY season, males increased their use of wooded areas (tree islands and willow/dense sawgrass) and decreased their use of wet prairie relative to WET season habitat use. Of the 11 males included in this analysis, six had a significant association between hydrologic season and habitat (chi-square test, $p<0.05$, df=3), and they typically

Table 3.6. Hydrologic season habitat use based on percentage of radio-locations in each habitat for the study sample of white-tailed deer in BCNP and ENP, November 1989 to March 1992.

	Female[a]		Male	
Habitat	WET	DRY	WET	DRY
Wet prairie	55 (5)[b]	56 (5)	28 (5)	17 (4)
Herbaceous prairie	18 (4)	16 (3)	20 (4)	20 (4)
Tree islands	17 (3)	18 (3)	35 (3)	41 (4)
Willow/dense sawgrass	11 (1)	12 (1)	17 (2)	22 (3)

[a] Sample sizes: female (24), male (11).
[b] Standard error in parentheses.

followed the same trend of increased use of wooded areas and decreased use of prairie in the DRY season, relative to the WET season.

3.4. Discussion

3.4.1. Annual Cycles

The most conspicuous observation regarding any of the spatial-use summary measures was the large variation among individuals and among years. Males tended to have slightly larger mean annual home ranges and mean straight-line distances between consecutive locations than females; however, this was negligible when individual variability was taken into account. This high variability among individuals may be due to a variety of factors such as resource availability (Byford 1969, Miller 1993), age (Gavin et al. 1984, Nelson and Mech 1984), concealment cover (Sparrowe and Springer 1970), weather (Michael 1970, Drolet 1976), and human disturbance (Sparrowe and Springer 1970). Local population dynamics such as density and social structure also may influence spatial-use patterns (Sanderson 1966, Gavin et al. 1984, Zultowsky 1992, Miller 1993). These deer exhibited a high degree of site fidelity, as evidenced by the small shifts in

annual home range centers, which measured <1 km for all deer. The strength of site fidelity in this population of deer during the time frame of the calibration data set also was discussed by Sargent (1992) and Zultowsky (1992). Labisky et al. (1999) noted the continuous maintenance of home ranges, even after the passage of Hurricane Andrew in August 1992.

The most prominent difference between spatial-use patterns of adult females and males was habitat selection. Females were twice as likely as males to be radio-located in the prairie, and males were twice as likely as females to be radio-located in a tree island or willow/dense sawgrass areas. This differential preference between females and males as evidenced by percentage of radio-locations in each habitat also is supported by the magnitude of the selection ratios calculated using radio-locations in the study site (Table 3.4). For many ungulates, differential use of food and cover resources by gender occurs as a result of differing energetic and reproductive strategies (Main and Coblentz 1990, Miquelle et al. 1992). Hydrophytic forbs (notably swamp lily, *Crinum americanum*), which contain high levels of crude protein (>15%) year-round (Loveless 1959a), comprised 68% of the annual diet of females in the study area (Hurd et al. 1995). Isolated patches of prairie that remain wet during the dry season support lilies and other forage important for pregnant and lactating does (Hunter 1990). Increased use of prairies also may provide protection against bobcat predation on fawns (Boulay 1992). Males consume a higher proportion of the woody browse and ferns found in the tree islands and wooded areas than females (Hurd et al. 1995). Males strive to maximize weight gain because increased body size leads to higher reproductive success (Clutton-Brock et al. 1982). Due to larger rumen size, males may require larger amounts of forage, but can subsist on

lower quality food (McCullough 1979, Shank 1982, Bowyer 1984, Beier 1987). Therefore, males focus foraging efforts on tree islands, which probably support higher forage biomass per unit area than other habitats (Miller 1993).

Females showed no significant trends for selection of home range content; however, males selected home ranges containing less wet prairie and more herbaceous prairie and wooded areas. Due to the polygynous nature of white-tailed deer, females are organized into matrilineal groups and tend not to disperse as juveniles, whereas males disperse from the family group at sexual maturity and establish new home ranges (Marchington and Hirth 1984). Therefore, males had an opportunity to select home ranges containing a higher proportion of their preferred habitats.

3.4.2. Hydrologic Seasons

Females traveled farther and had larger home ranges in the dry season than the wet season, possibly because of limitations in nearby available forage during the winter drought. Typically, white-tailed deer concentrate activities when food is plentiful and expand activities when food is scarce (Byford 1969). However, no changes in the habitat-use patterns of females between the wet and dry seasons were evident.

Males traveled more, had larger home ranges, increased their use of wet prairie, and decreased their use of tree islands in the wet season relative to the dry season. Because the wet season includes the rutting period, during which time males are searching for females to breed, they travel greater distances to find females and utilize the landscape matrix of wet prairie more heavily in those search efforts. During the seasonal hunt, which occurs during the early dry season, males, especially those in BCNP, may increase their use of wooded areas to obtain a higher degree of concealment cover.

CHAPTER 4
DEVELOPMENT, CALIBRATION, AND EVALUATION OF THE SIMULATION MODEL

In this chapter, I present and demonstrate the approach developed to calibrate an IBSE simulation model. Specific issues with regards to model calibration are addressed and then introduced as steps of an iterative process to attain a satisfactory simulation model. Finally, parameterization of the final simulation model is described. I developed the simulation using C++ (Borland C++ Builder 3.0, Inprise Inc.) with object-oriented programming techniques.

4.1. Approach and Technique

Determining correct model form (verification) involves evaluating the conceptual structure and the transformation of the structure into computer algorithms (Bart 1995, Conroy et al. 1995, Rykiel 1996). Model structure is often visualized through flow charts (Fig. 4.1). Detailed literature review and analyses of additional data aid the verification of correct conceptual model structure. Assuming the model structure is correct, the calibration process consists of altering parameter values until the modeled system is represented adequately. Model calibration also may reveal algorithms in the simulation model that need to be modified if the optimum parameterization of the algorithm is not sufficient. Updating algorithms and parameter values is an iterative process, requiring constant reevaluation of the simulation model.

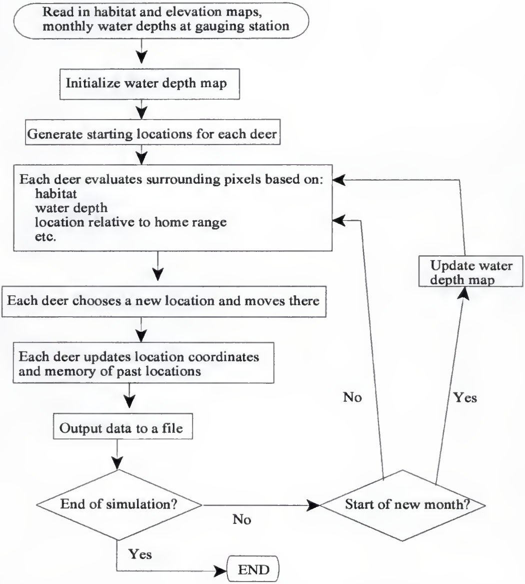

Figure 4.1. Simulation flow chart to aid in visualization of model structure. Example depicts white-tailed deer movement in the Florida Everglades.

During the development of this model building process, I chose to focus on several issues. Parameterization of the movement process is approached by quantitatively and visually evaluating various movement algorithms. An approach for evaluation of potential movement algorithms relative to the observed field data is presented. To address algorithm and parameter value evaluation, simulation experiments are conducted, and simulated and observed data are compared quantitatively with discrepancy measures. However, before quantitative model evaluation is performed, the amount of time (i.e., number of iterations) the simulation must run before meaningful testing can occur must be determined. Qualitative evaluation (e.g., visual comparison) also is an important component of model calibration. Once the simulated data approach the observed data, the robustness of the simulation to represent the observed data is evaluated.

4.1.1. Parameterization of Animal Movement

Observed movement patterns are a function of many possible factors, which vary from individual to individual. Some of these factors may include age, predator threat, availability of food and water, location of neighboring individuals (of the same or different species), surrounding micro- and macro-habitat, weather, time of year, and time of day. Differences in individual preferences and random chance also may influence movement decisions. Many of these potential influences can be measured (i.e., weather conditions and habitat availability), and potential relationships between these factors and the movement patterns can be explored (i.e., correlation analyses and habitat-selection ratios). However, often these factors cannot be measured on the scale appropriate for the parameters of interest, and some factors may be unmeasurable or unknown.

Radio-telemetry data collected from individual animals can provide some of this information (White and Garrott 1990). These data are used to evaluate individual patterns of movement, home range size and shape, and habitat use. However, these summary statistics are 'outcomes' resulting from the movement patterns generated by a multitude of factors. Statistical analyses can identify associations between the environmental factors and the measured outcomes. These associations help in formulating testable hypotheses regarding how environmental factors may affect movement patterns, and, thus, affect the measured outcomes. This approach is useful in developing a simulation of animal movement patterns. Based on knowledge of the natural history of the species and the results of the data analyses, rules to simulate movement patterns can be developed. These rules then can be tested by comparing the measured 'outcomes' from the real individuals and the 'outcomes' of the simulated individuals.

Simulating animal movement paths is accomplished with any of several approaches. Vector-based models, in which a simulated individual chooses a movement direction and, often, a movement distance for each step, constitute one approach. The direction and distance for each move are chosen, based on those surrounding environmental factors deemed important to movement decisions. Grid-based models, in which simulated individuals move among pixels on a grid superimposed over the landscape, constitute a second approach. These vector- or grid-based simulation models can be either deterministic or stochastic. Deterministic models are designed such that the individual always makes the 'best' movement decision (i.e., always moves in the direction of best habitat). In contrast, stochastic models use random draws from various probability distributions based on those factors that influence movement decisions, such

that individuals are most likely to make the 'best' choice. For the model presented in this study, I used the grid-based stochastic simulation approach.

4.1.2. Measuring Model Fit

Model fit is evaluated by comparing simulated outcomes of the model and observed outcomes of the field data. These quantities, often termed discrepancy measures (DMs), quantify the difference between a simulated data set and an observed data set and have the general form:

$$D(x) = g(P(x), O)$$

where $P(x)$ is a summary statistic for one run of the simulation with parameter set x, x is an element of $\mathbf{X}$ (the set of all feasible model parameters), and O is the summary statistic computed for the observed data (Van der Molen and Pintér 1993). The objective of model calibration is to minimize the DM(s). DMs may be calculated for summary statistics such as average home range size or the percentage of time individuals are located in specific habitat types.

One family of DMs takes the form:

$$D(x) = |P(x) - O|^{\beta}$$

where $\beta>0$ (Van der Molen and Pintér 1993). For example, if $\beta=1$, $D(x)$ is the absolute value of the deviation between simulated and observed summary statistics, and if $\beta=2$, $D(x)$ is the squared deviation between simulated and observed summary statistics. Evaluation of summary statistics, such as mean annual home range size or mean distance

between consecutive annual home range centers, is accomplished with this family of DMs.

A DM useful for evaluating a set of *n* dependent outcomes, such as the percentage of radio-locations in each habitat, has the form:

$$D(x) = \sum_{i=1}^{n} \frac{\left(P_i(x) - O_i\right)^2}{O_i}$$

where O_i is the summary statistic for the observed data for the i^{th} outcome, $P_i(x)$ is the i^{th} summary statistic for a run of the simulation with parameter set x, and x is an element of **X** (the set of all feasible model parameters). This DM approximates a chi-square goodness-of-fit statistic with $n-1$ degrees of freedom where $P_i(x)$ and O_i are the percentage of occurrences in habitat i based on simulated and observed individuals, respectively. Mayer and Butler (1993), Power (1993), and Van der Molen and Pintér (1993) provide additional forms for discrepancy measures.

4.1.3. Visual Assessment

An additional component of model verification and calibration is the visual comparison of simulation output and observed data. Even if the discrepancy measures based on summary statistics demonstrate that simulation output is comparable to observed data, movement patterns also must be visually realistic based on knowledge of the natural history and ecology of the species.

4.1.4. Experimental Design

Simulation experiments are conducted to identify a set of algorithms and parameter values that minimizes discrepancies between simulated and observed data. In this setting, each algorithm and parameter value to be evaluated is a factor in the experiment, and an experimental unit (EU) is one run of the simulation model. When evaluating large numbers of model parameters, effects of each parameter on simulation outcomes can be complicated and difficult to identify. Factorial experiments allow for the simultaneous investigation of the effects of many factors (i.e., simulation model parameters). Moreover, the ensuing analysis of variance (ANOVA) of the simulation data can include interaction terms that explain the interrelationship among the simulation parameters. However, as the number of investigated factors increases, the number of EUs required to examine all factor combinations increases rapidly. For example, a factorial experiment having p factors, each with k levels, requires k^p EUs for one replicate. Experimental designs have been developed that make efficient use of resources by requiring a minimal number of EUs. Response surface methodology (Khuri and Cornell 1987, Montgomery 1991) also provides a collection of specific experimental designs and statistical techniques to facilitate the estimation of factor settings that optimize a response variable.

Often a sequence of experiments is necessary to optimize simulation model algorithms and parameters, with the analysis of each experiment dictating the particulars of the following experiment. First-order designs are initial screening experiments used to estimate and test main effects and interactions among the factors. Common designs are 2^p factorials and fractions of 2^p factorials (Cochran and Cox 1957, Montgomery 1991).

Fractional factorials reduce the number of required EUs using the assumption that higher-order interactions (i.e., 3- and 4-way interactions) are negligible. The response variables from each EU are analyzed using ANOVA. For the model development process presented in this study, the response variables are DMs (Section 4.1.2), and the goal of optimization is to attain values of these DMs close to zero. If an optimum is not attained inside the initial experimental region, the method of steepest descent is used to establish parameter settings for a subsequent experiment more likely to contain a minimum (Khuri and Cornell 1987, Montgomery 1991). This process is repeated until a minimum is achieved, which results in a sequence of experiments.

When statistical analyses indicate that the design settings are close to an optimum, additional experimentation is performed to identify a set of parameter settings that minimizes the DM (a local minimum). More specifically, a second-order design, estimating main effects, first-order interactions and quadratic effects, is often required to approximate the curvature of the true response surface. Common second-order designs are central composite designs, 3^p factorials, and 3^p fractional factorials (Cochran and Cox 1957, Khuri and Cornell 1987).

4.1.5. Simulation Burn-in Time

The "burn-in" period (Fig. 4.2) is the number of iterations required for the simulation to reach a steady-state (Kleijnen 1987). A population-based stochastic model is said to have a statistically stationary state if the probability distribution of population size is constant over a long time interval (Nisbet and Gurney 1982). When generalized to all population- and individually-based simulation models, the burn-in period is completed when a statistically stationary state is reached by all relevant outcome measures.

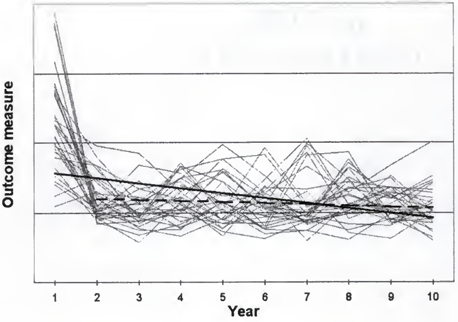

Figure 4.2. Example of burn-in time estimation for a simulation outcome measured on an annual basis. Individual outcomes are plotted in grey; linear slope is significantly different from zero when estimated for all years (heavy solid black line) and not significantly different from zero when using data from years 2 through 10 (heavy dashed black line).

Estimation of burn-in time is important for several reasons. First, if the goal of the modeling effort is to explore the impacts of perturbations on the simulation outcomes, the simulation must be in a steady-state before applying the perturbations. If it is not in a steady-state, the effects of burn-in and the perturbations on the simulation outcomes are confounded (i.e., confused and inseparable). Second, if the goal of the modeling effort is to explore impacts of introduction or reintroduction of a species in a particular geographic region, then determining if a steady-state is reached is essential. If it is determined that a steady-state is reached, estimating the time until that steady-state is reached is also important.

Burn-in time is estimated by running the simulation for an extended period of time and examining temporal trends and autocorrelations of simulation "outcomes" for each individual (Fig 4.2). The approach for this study utilizes repeated measures analyses to identify significant time trends in the summary outcome (Diggle et al. 1994, Littell et al. 1996, Vonesh and Chinchilli 1997). If no significant linear time trend over the entire simulation interval is present, burn-in time has no effect on that particular outcome. A significant linear time trend is evidence that simulation burn-in affects the outcome measure. In this case, the test for a linear trend is repeated using all the time intervals except the first. If the second test for a time trend is not statistically significant, burn-in time is established at one interval; otherwise, the linear trend test is repeated excluding the first and second time intervals. These steps continue until there is no longer a significant linear time trend. If the simulation has not reached a steady-state until the end of the simulated time period or never reaches a steady-state (i.e., simulation burn-in time is equal to or longer than the time period of the simulation), further exploration of burn-in time and the form of the simulation algorithms is necessary. For each test for linear trend, an α-level of 0.01 was used. Because of multiple and sequential testing, this slightly more conservative α-level was used to reduce Type I error rates.

4.1.6. Final Model Evaluation

In all model-building exercises, evaluating goodness-of-fit of the final model is crucial. For models such as regression, analysis of variance, and generalized linear models, fit often is evaluated with the coefficient of determination (R^2), Akaike's Information Criterion [AIC (Akaike 1974)] , and chi-square goodness-of-fit tests. However, these tools are not applicable for Monte Carlo simulations, such as the IBSE

simulation developed in this dissertation. To evaluate the simulation results, I test the likelihood of values of the observed outcomes arising as realizations of the posited stochastic model using estimated p-values from an estimated predictive distribution (Rao 1977, Bjørnstad 1990, Gelman et al. 1995). First, the general approach is described, and then the adaptation of this method used for evaluating the IBSE simulation model is presented.

Let $y_1, y_2, y_3, \ldots, y_n$ be the observed data, where each y_i is either a vector or a scalar variable and n is the number of observations. Also let θ be the vector of unknown parameters in the model, and $f(y_1, y_2, y_3, \ldots, y_n|\theta)$ be the density (i.e., the joint distribution of $y_1, y_2, y_3, \ldots, y_n$ given θ). Inferences regarding some subsequent observation, y^*, can be made using the predictive density function (PDF):

$$f\left(y^* \middle| y_1, y_2, y_3, \ldots, y_n, \theta\right)$$

If θ is known then the PDF provides all the information regarding inferences on y^*. If θ is unknown, one approach to making inferences on y^* is to estimate θ and substitute the estimate for θ in the PDF. The parameter, θ, can be estimated from

$$f\left(y_1, y_2, y_3, \ldots, y_n | \theta\right)$$

using maximum likelihood or some other estimation method. Using this estimated value for θ, the estimated predictive density function (EPDF)

$$f\left(y^* \middle| y_1, y_2, y_3, \ldots, y_n, \hat{\theta}\right)$$

can then be used to make inferences about y^*. Using the EPDF with a known form and an

estimated θ to make inferences about y^* is misleadingly precise and results in predictive p-values that are more extreme than if θ were known (Aitchison and Dunsmore 1975).

For the simulation model developed in this study, $y_1, y_2, y_3, \ldots, y_n$ represent the summary outcomes (e.g., mean annual home range size and mean percentage of observations in each of the habitats) from n runs of the simulation model, θ is the vector of unknown model parameters (e.g., number of steps per day, relative affinities for habitat, and relative affinities based on water depths), and y^* is the summary outcome from observed field data. Of interest is the likelihood that the value of y^* could have arisen as an outcome of the simulation model. Assuming y^* is independent of $y_1, y_2, y_3, \ldots, y_n$, the EPDF simplifies to

$$f\left(y^* \middle| \hat{\theta}\right)$$

where $\hat{\theta}$ is provided by the calibration process. The likelihood that the value of y^* could have arisen from the posited simulation model can be measured by the tail-area probability:

$$\min\left[\Pr\left(Y \leq y^* \middle| \hat{\theta}\right), \Pr\left(Y \geq y^* \middle| \hat{\theta}\right)\right]$$

Because the empirical form of the EPDF is unknown, the predictive p-value is estimated by an approximate distribution obtained through Monte Carlo simulation. Multiple runs of the IBSE simulation model are conducted and the distribution of the simulated outcomes is used to estimate the tail-area probability (Fig. 4.3).

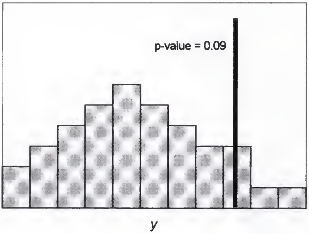

Figure 4.3. Example of an approximate EPDF. Histogram represents the distribution of 100 outcomes obtained by Monte Carlo simulation. A subsequent observation, y^*, is represented by the vertical line and the approximate tail-area probability is 0.09.

4.1.7. Details of the Iterative Approach

An iterative process is used to calibrate the simulation model (Fig. 4.4). Initial movement algorithms and parameter values are selected for the first experiment. Once the experimental design is selected and the simulation runs are completed, burn-in time is evaluated for each summary outcome for each EU. Experiment burn-in time is estimated as the maximum burn-in time of all evaluated summary outcomes for all EUs. Statistical analyses are performed on each discrepancy measure from the time interval (i.e., annual cycle) following estimated experiment burn-in time. Based on the results of these analyses and subjective opinions from viewing simulation output, settings for the next simulation experiment are determined. Movement algorithms are changed or parameter values are adjusted, as appropriate, in subsequent experiments. When the discrepancy measures appear to be minimized, multiple runs of the simulation with the same

parameter values are conducted and the distributions of the simulated summary statistics, relative to the observed summary statistics, are evaluated using predictive p-values.

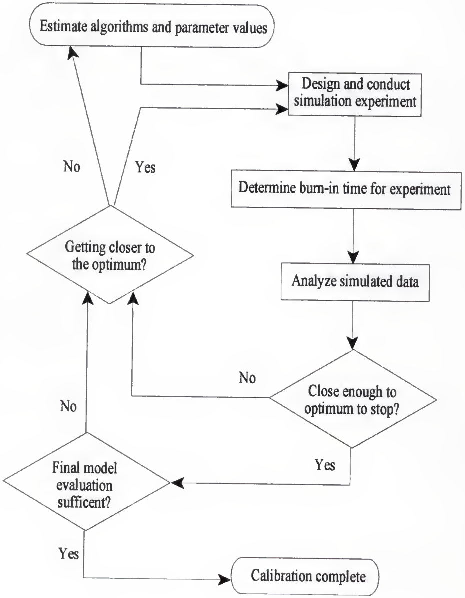

Figure 4.4. Flow chart representing the iterative process of model calibration.

4.2. Initial Model Parameterization

This first series of calibration experiments focused on parameterization of the adult female movement process. Once female movements were sufficiently calibrated, the algorithms and parameters were adjusted for calibration of the male movement process.

In the movement process that was developed, each deer made multiple moves per day. In order to make valid comparisons of the simulated data and the observed field data, only some locations of the simulated deer (i.e., one radio-location every 5 days) were used for calculation of the outcome summary statistics. These statistics included home range size, distance between consecutive annual home range centers, distance between two consecutive radio-locations (5 days apart), and percentage of observations in each habitat.

Initial locations of simulated deer were representative of home range centers of observed deer from the calibration data set. The habitat map over which deer moved was a closed environment (i.e., deer could not move off the map); however, there was no 'repelling force' to prevent them from moving to the edge of the map. Simulated deer that moved adjacent to the map boundary had fewer pixels from which to choose for their next location since there was a zero probability of moving to a pixel not within the study area. These deer that formed home ranges on the boundary of the habitat map may not have had realistic movement patterns; therefore, they were removed from data analyses for model calibration.

4.2.1. Movement Step Size

The habitat map was created using 20-m pixels; however, there were several problems simulating deer movements on a scale that small. Simulated deer that moved a

maximum distance of one pixel per step (to one of the eight neighboring pixels or to the current location) had to make a very large number of steps to cover a sufficient portion of its home range over a 5-day period. Also, simulated deer were stranded in large regions of continuous habitat (e.g., large areas of prairie) and wandered randomly, never finding other habitats. Although some observed deer spent nearly all their time in the prairie, a high proportion of the deer in early simulations exhibited this behavior. One alternative possibility was to allow deer to move farther than one pixel per step. Although deer traveled longer distances during one day, they would 'jump' from one location to another, leaving 'holes' in the memory of its previous locations. These simulated deer tended to wander over the entire landscape, probably because home range formation is partly based on an algorithm using memory of previous locations.

To address this problem, a single iteration of simulated deer movement was developed as a two-stage process. First, deer selected a new location, using pixels larger than 20-m, and then selected a 20-m pixel within the large pixel. Because the dynamics of the simulated movements changed drastically as the size of the large pixel changed, evaluation of the potential pixel sizes quantitatively would require developing an optimum set of parameters for each pixel size and then comparing the optimized models. This approach was not feasible given the amount of computer time needed to optimize a single simulation model. Thus, the size of the large pixel was chosen to be 60-m for several more qualitative reasons. An average home range of 300 ha contained approximately 7500 20-m pixels, 1875 40-m pixels, 833 60-m pixels, 469 80-m pixels, 300 100-m pixels, or 20 500-m pixels. Small pixel sizes required deer to make a large number of movements to cover most of the home range during a reasonable time interval.

Large pixel sizes required fewer movements to cover most or all of the home range; however, these large pixels also drastically reduced the resolution of the habitat map. Use of a lower resolution when developing the habitat map would have caused the loss of many of the small tree islands and other small features of the landscape (K. E. Miller, personal communication). If the large pixels used in the simulation model were 'too large', simulated deer were less likely to find and utilize the smaller habitat features. A compromise between the two extreme scenarios was to develop the simulation with 60-m large pixels, each containing nine 20-m small pixels (Fig. 4.5).

In summary, simulated deer made multiple movements over a 5-day interval, the interval over which simulated 'radio-locations' were taken. In the first stage of each movement iteration, using 60-m pixels, deer moved a maximum distance of one pixel in

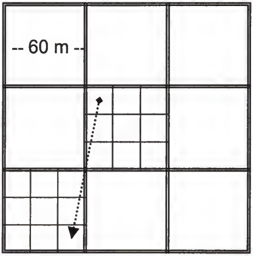

Figure 4.5. Two-stage movement process of a simulated deer using large 60-m pixels. The hypothetical deer moved from the upper left 20-m pixel in the center 60-m pixel to the lower right 20-m pixel in the lower left 60-m pixel.

any direction. During this stage, a deer evaluated its surroundings and determined the probability of moving to each pixel based on habitat, water depth, and relative location in its home range. The second stage consisted of selecting a 20-m pixel, based on habitat and water depth, within the 60-m pixel.

4.2.2. 60-m Movement Stage

In the first stage of a movement step, each deer evaluated its surroundings based on habitat, water depth, and relative location in its home range. A relative affinity score, a continuous, ratio variable, was assigned to each pixel for each factor. For example, if a deer had to choose between two pixels, with relative affinity scores of 5 and 10, it would be twice as likely to move to the pixel with a relative affinity of 10 than it would be to move to the pixel with a relative affinity of 5. These scores were converted to probabilities of moving to given pixels and averaged, using methods detailed below. Final values for the relative affinity scores for each factor were determined during the calibration process.

4.2.2.a. Habitat

Each 20-m pixel was assigned a relative affinity score based on habitat contained inside the pixel. Initial values for the relative affinities (Table 4.1) were updated throughout the calibration process. Relative affinity scores for the 60-m pixels were determined using the mean relative affinity of the nine 20-m pixels it contained. The mean relative affinity score for each 60-m pixel was standardized by converting it to a probability:

$$p_j = \frac{affinity_j}{\sum_{j=1}^{9} affinity_j}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_j was the probability of moving to pixel j based solely on habitat, and $affinity_j$ was the relative affinity score for pixel j. For example, if the nine 60-m pixels to which a simulated deer could move had relative affinity scores for habitat of 20, 30, 40, 10, 10, 50, 50, 20, and 30, then the probability of moving to each pixel based on habitat would be 0.08, 0.11, 0.15, 0.04, 0.04, 0.19, 0.19, 0.08, and 0.11, respectively.

Table 4.1. Initial habitat relative affinity scores.

Habitat	Symbol	Relative affinity
Wet prairie	A_{WPR}	10
Herbaceous prairie	A_{HPR}	20
Tree island	A_{TRE}	50
Willow/dense sawgrass	A_{WSA}	50
Cypress prairie/strand	A_{CYS}	10
Pine	A_{PIN}	10
Mangrove	A_{MAN}	1

4.2.2.b. Water depth

Water depth in each 20-m pixel was calculated from the water depth at P-34 (centrally located water gauge) and the relative elevations of each habitat (Section 2.2.2). For model calibration, an annual water depth cycle was repeated for each year of the simulation. This annual cycle was based on the average monthly water depth at P-34 during the collection of model calibration data (Table 4.2).

Water depth in each 60-m pixel was calculated as the mean depth of water in the nine 20-m pixels it contained. A relative affinity score for each pixel was calculated as

$$affinity_j = \begin{cases} \alpha & \text{if depth} < \beta \\ \alpha - \left[\left(\dfrac{\alpha - 1}{\gamma - \beta}\right)(\text{depth} - \beta)\right] & \text{if } \beta \leq \text{depth} \leq \gamma \\ 1 & \text{if depth} > \gamma \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$ and where α, β, and γ were the parameters with values determined during the calibration process (Fig. 4.6). The relative affinity for each pixel was standardized by converting it to a probability:

$$p_j = \frac{affinity_j}{\sum_{j=1}^{9} affinity_j}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_j was the probability of moving to pixel j based solely on water depth, and $affinity_j$ was the relative affinity score for pixel j.

Table 4.2. Monthly water depths at P-34 for one annual cycle of the calibration simulation, using average water depths for each month from April 1989 to March 1992.

Month	Depth (cm)	Month	Depth (cm)
April	-40.78	October	20.56
May	-30.00	November	10.81
June	-0.06	December	-1.50
July	19.79	January	-9.42
August	27.99	February	-16.39
September	28.51	March	-27.10

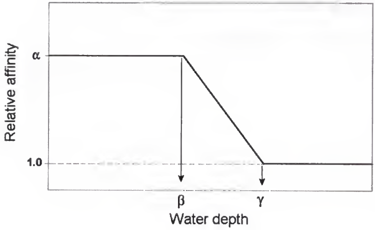

Figure 4.6. Relationship between water depth and relative affinity for moving to a particular pixel, with the minimum affinity score set at 1. α, β, and γ were parameters optimized in the model calibration.

4.2.2.c. Home range

Two algorithms utilizing the previous locations of a deer induce the formation and maintenance of home ranges. A homing beacon encouraged movement towards the center of the home range, and pixel memory encouraged deer to move to pixels visited in their recent past (e.g., 2 months). A combination of the two algorithms was utilized because neither performed adequately when used alone. The homing beacon produced circular home ranges with little variation in size, and the pixel memory algorithm was not strong enough to maintain the strong site fidelity of these deer. However, together these algorithms produced home ranges that varied in shape and size and that maintained a realistic degree of site fidelity in the simulated deer.

The homing beacon algorithm provided simulated deer with a stronger affinity for pixels closer to their homing beacon, $\left(\bar{x}_{\text{home}}, \bar{y}_{\text{home}}\right)$, than away from their homing

beacon. The location of the homing beacon, based on *k* previous radio-location coordinates (one taken every 5 days), was updated every 5 days using the moving averages:

$$\bar{x}_{\text{home}} = \frac{1}{k}\left(x_t + x_{t-1} + x_{t-2} + \ldots + x_{t-k+1}\right)$$
$$\bar{y}_{\text{home}} = \frac{1}{k}\left(y_t + y_{t-1} + y_{t-2} + \ldots + y_{t-k+1}\right)$$

where (x_t, y_t) were the coordinates of the most recent radio-location and (x_{t-1}, y_{t-1}) were the coordinates of the radio-location taken 5 days earlier, etc. The window of time used to calculate the location of the homing beacon encompassed the *k* prior radio-locations.

The relative affinity scores for the nine 60-m pixels to which the deer could move were based on the direction of travel from the current location of the individual deer to the homing beacon (Fig. 4.7). To avoid simulated deer from gradually shrinking their home ranges due to a concentration of movements around the homing beacon, the strength of the beacon, δ (equal to 1, $\frac{1+\phi}{2}$, or ϕ), was reduced exponentially as a deer moved closer to its beacon:

$$affinity_j = \begin{cases} \delta^{z/\mu} & \text{if } z < \mu \\ \delta & \text{otherwise} \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$, and where δ or $\delta^{z/\mu}$ was the relative affinity score, μ was the distance from the homing beacon at which relative affinity was constant, and *z* was the distance from the current location to the homing beacon. The final values for ϕ (>0) and μ (>0) were estimated through model calibration; in initial simulations, ϕ=3 and μ=750 m.

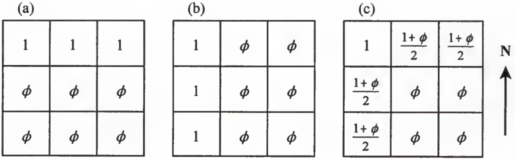

Figure 4.7. Illustration of relative affinity calculations for the homing beacon, with the homing beacon located southeast of the current location [center pixel of (a), (b), and (c)]. Affinity scores to move (a) towards the south and (b) towards the east were averaged to give (c) δ (equal to 1, $\frac{1+\phi}{2}$, or ϕ) which was used to calculate the relative affinity scores of moving to each of the nine possible pixels.

The pixel memory algorithm provided simulated deer with a stronger affinity for previously visited pixels than for those not visited in the recent past. The relative affinity score for pixel j was defined as

$$affinity_j = \begin{cases} \lambda & \text{if pixel } j \text{ visited during known memory} \\ 1 & \text{otherwise} \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$ and where λ (>1) was the relative affinity. Each simulated deer had a map of its recent locations created with a moving window, containing all previous locations of a deer for a given period of time (e.g., 2 months). This map was used to assign relative affinity scores for each of the nine 60-m pixels a deer evaluated for each step. The final value for λ was estimated through model calibration; in the initial simulations, λ=4.

The relative affinity scores for the homing beacon algorithm and for the pixel memory algorithm for each of the nine 60-m pixels were standardized by converting them to probabilities:

$$p_j = \frac{affinity_j}{\sum_{j=1}^{9} affinity_j}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_j was the probability of moving to pixel j and $affinity_j$ was the relative affinity score for pixel j either for homing beacon or for pixel memory.

4.2.2.d. Combining movement factors

The probability of moving to each of the nine 60-m pixels was calculated, for each of the four algorithms as described above. For each pixel, the probabilities for each factor were averaged to give the probability of moving to each pixel:

$$\pi_j = \frac{1}{4}\sum_{i=1}^{4} p_{ij}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_{1j}, p_{2j}, p_{3j}, and p_{4j} were probabilities of moving to pixel j based on habitat, water depth, homing beacon, and pixel memory, respectively. The deer chose a 60-m pixel for its next location based on a random draw from the multinomial distribution $(\pi_1, \pi_2, \pi_3, \ldots, \pi_9)$.

4.2.3. 20-m Movement Stage

The nine 20-m pixels contained inside the 60-m pixel of the location of the deer were evaluated based on habitat and water depth. Relative affinity scores were used to calculate the probabilities of moving to each 20-m pixel based habitat and based on water depth. These probabilities were averaged to obtain the probability of moving to each of

the nine 20-m pixels:

$$\pi'_j = \frac{1}{2}\left(p'_{1j} + p'_{2j}\right)$$

for $j = 1, 2, 3, \ldots, 9$ and where p'_{1j} and p'_{2j} were the probabilities of moving to the 20-m pixel j based on habitat and water depth, respectively. The deer selected a 20-m pixel based on a random draw from the multinomial distribution $(\pi'_1, \pi'_2, \pi'_3, \ldots, \pi'_9)$.

4.2.4. Simulation Initialization

The simulation began with 30 deer in a set of specified locations that were representative of the home range centers of the deer included in the calibration data set. Each deer started the simulation with no history or memory of previous locations. During the time deer were building their initial memory map and homing beacon coordinates, their movements were a function of habitat and water depth only. Once the simulation ran for the length of the memory of a deer (e.g., 2 months), a deer began to use the home range algorithms in its movement steps.

4.3. Model Calibration Experiments

In this section, the first two of a series of calibration experiments for females were discussed. In these two experiments, only annual summary outcomes were evaluated; however, data from later experiments were analyzed to explore and calibrate seasonal patterns. These two experiments and subsequent experiments for females were described in Appendix C, and calibration experiments for males were discussed in Appendix D.

4.3.1. First Calibration Experiment

The first experiment focused on the number of two-stage movement steps over a 5-day interval and parameter values for the home range algorithms (Table 4.3). A one-half fraction of a 2^6 factorial design (i.e., 2^{6-1} fractional factorial) was used. This design allowed estimation of all main effects and first-order interactions with 10 degrees of freedom for experimental error, assuming higher-order interactions were negligible. Each of the 32 EUs consisted of 30 deer with same starting coordinates, located in areas where the majority of the study deer had resided.

Table 4.3. Factor levels for the first calibration experiment.

Factor description	Symbol	Low	High
Maximum affinity for homing beacon	ϕ	3	5
Distance (m) from homing beacon at which affinity is ϕ	μ	750	1750
Relative affinity for previously visited pixels	λ	4	12
Memory length (5-day intervals)	ML	12	36
Number of steps per 5-day interval	STEP	100	300
Relative affinity score for tree islands and willow/dense sawgrass	$A_{TRE,WSA}$	30	50

The movement algorithms in this experiment were those discussed in Section 4.2 with the exception of water depth. Since simulation burn-in time may have been confounded with temporal effects of water levels, seasonally fluctuating parameters and algorithms were not included. After several experiments were completed and a reference value for burn-in time was estimated, water depth was included as a factor in the simulation experiments (Table C.6). Until water depth was included in the model, the probability of moving to each large-scale pixel was calculated as

$$\pi_j = \frac{1}{2}p_{1j} + \frac{1}{4}p_{2j} + \frac{1}{4}p_{3j}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_{1j}, p_{2j}, and p_{3j} were the probabilities of moving to pixel j based on habitat, homing beacon, and location memory, respectively.

Simulations were run for an extended period of time to adequately estimate burn-in time. At this stage of calibration of the simulation model, the main focus was to simulate movement patterns of deer and understand the temporal and spatial dynamics of the movement algorithms. Although longer than the expected life span of a white-tailed deer, each EU was run for 15 years. Based on preliminary simulations, a simulation length of 15 years was sufficient to determine if and when a steady-state had been reached by the outcome measures (e.g., annual home range size and percentage of observations in each habitat). Incorporating additional dynamics, such as recruitment and mortality, would make the simulation more realistic, but adequate evaluation of the dynamics of the movement algorithms would be difficult because of the potential for confounding. Additionally, only 1 year of data (the year following experiment burn-in) from of each EU was used for analysis of the factorial experiment, thus minimizing the effect of population dynamics examined simulation outcomes.

For the simulated data to be comparable to observed data, 72 locations per year (1 per 5 days) were used to calculate outcome measures. Annual home range size, distance between consecutive annual centers of activity, mean distance between consecutive locations, and percentage of observations in each habitat were calculated and used as outcome statistics.

A series of repeated measures ANOVAs was performed on the annual outcome measures to estimate burn-in time. A separate analysis for each outcome for each of the 32 EUs was performed. These outcomes were annual home range size, distance between consecutive annual centers of activity, mean distance between consecutive locations, and percentage of radio-locations in each of the four major habitats in the study area (i.e., wet prairie, herbaceous prairie, tree islands, and willow/dense sawgrass). Several covariance structures were evaluated before testing specific hypotheses regarding temporal trends. Compound symmetry assumed equal correlation among all years. An auto-correlation structure assumed correlation among years was a function of "distance" between any pair of years (i.e., the correlation between outcomes from year *i* and year *j* was equal to $\rho^{|i-j|}$). A heterogenous auto-correlation structure was similar to an auto-correlation structure, with additional parameters to estimate variances for each year. Akaike Information Criterion values (AICs), log-likelihood values penalized for the number of estimated parameters (Akaike 1974), were compared to determine the most appropriate structure for each outcome measure. For distance between consecutive annual centers of activity, mean distance between consecutive locations, and percentage of radio-locations in each of the four major habitats, the auto-correlation structure provided the best fit. For annual home range size, the heterogenous auto-correlation structure provided the best fit. Tests for linear time trends were used to estimate burn-in time for each EU for each outcome. Based on an α-level of 0.01, the maximum burn-in time was estimated at 4 years, so summary data from the 5th year of simulation were used to evaluate the adequacy of the simulation model parameters (Tables 4.4 and 4.5). Data from the 6th year to the 15th year of the simulations were not used in the following analyses.

Table 4.4. Summary outcome measures of home range size, distance between consecutive home range centers, and distance between consecutive locations from first calibration experiment for adult females from the 5th year of simulation.

ϕ	μ	λ	ML	STEP	$A_{TRE,WSA}$	Home range size (ha)	Annual center shift (m)	5-day distance (m)
3	750	4	12	100	30	563	1134	486
3	750	4	12	300	50	709	1181	737
3	750	4	36	100	50	502	703	503
3	750	4	36	300	30	815	453	800
3	750	12	12	100	50	436	913	458
3	750	12	12	300	30	734	920	738
3	750	12	36	100	30	543	1118	465
3	750	12	36	300	50	539	681	685
3	1750	4	12	100	50	792	1460	499
3	1750	4	12	300	30	1426	1523	830
3	1750	4	36	100	30	715	862	524
3	1750	4	36	300	50	1044	588	842
3	1750	12	12	100	30	698	1411	482
3	1750	12	12	300	50	953	1292	741
3	1750	12	36	100	50	638	1381	470
3	1750	12	36	300	30	1058	1318	776
5	750	4	12	100	50	428	538	496
5	750	4	12	300	30	568	351	747
5	750	4	36	100	30	474	646	509
5	750	4	36	300	50	538	372	734
5	750	12	12	100	30	397	432	499
5	750	12	12	300	50	474	362	724
5	750	12	36	100	50	356	424	481
5	750	12	36	300	30	519	337	721
5	1750	4	12	100	30	662	625	530
5	1750	4	12	300	50	831	565	826
5	1750	4	36	100	50	528	746	493
5	1750	4	36	300	30	951	504	847
5	1750	12	12	100	50	487	710	487
5	1750	12	12	300	30	908	568	819
5	1750	12	36	100	30	556	589	502
5	1750	12	36	300	50	785	536	790

Table 4.5. Summary outcome measures of percentage of radio-locations in each habitat[a] from first calibration experiment for adult females from the 5th year of simulation.

ϕ	μ	λ	ML	STEP	$A_{TRE,WSA}$	Percentage of radio-locations in each habitat					
						WPR	HPR	TRE	WSA	CYP	MAN
3	750	4	12	100	30	37.2	33.0	14.5	3.3	5.0	0.6
3	750	4	12	300	50	32.7	23.2	26.5	4.8	4.4	0.0
3	750	4	36	100	50	43.0	17.3	24.2	4.2	1.7	0.2
3	750	4	36	300	30	40.3	27.5	21.9	3.4	0.9	0.0
3	750	12	12	100	50	28.1	24.6	32.0	4.6	1.5	0.1
3	750	12	12	300	30	31.1	30.2	23.8	4.1	3.3	0.0
3	750	12	36	100	30	43.5	22.9	19.0	2.1	5.0	0.2
3	750	12	36	300	50	24.3	24.2	33.7	5.8	2.3	0.1
3	1750	4	12	100	50	36.9	18.1	26.2	4.0	6.3	1.0
3	1750	4	12	300	30	34.1	33.1	16.6	3.1	4.7	0.1
3	1750	4	36	100	30	48.2	21.6	16.1	3.1	1.3	0.0
3	1750	4	36	300	50	29.3	29.8	24.9	4.6	3.7	0.0
3	1750	12	12	100	30	38.0	28.4	17.4	3.1	5.6	0.2
3	1750	12	12	300	50	23.3	28.2	34.2	5.0	1.1	0.1
3	1750	12	36	100	50	41.5	16.5	20.1	4.1	6.3	0.7
3	1750	12	36	300	30	38.3	26.9	19.5	3.8	4.7	0.0
5	750	4	12	100	50	30.3	28.6	23.6	3.7	4.1	0.9
5	750	4	12	300	30	43.1	31.2	16.9	2.6	0.8	0.0
5	750	4	36	100	30	46.7	28.5	15.4	2.8	0.5	0.0
5	750	4	36	300	50	31.9	21.6	27.5	5.3	0.9	0.0
5	750	12	12	100	30	42.6	28.4	16.5	2.6	3.1	0.2
5	750	12	12	300	50	33.6	21.9	28.3	4.8	1.9	0.0
5	750	12	36	100	50	45.0	14.4	25.3	5.3	1.7	0.1
5	750	12	36	300	30	30.2	31.5	28.5	3.0	1.4	0.3
5	1750	4	12	100	30	43.5	31.3	15.9	2.1	1.4	0.1
5	1750	4	12	300	50	34.1	20.6	29.2	5.3	2.4	0.2
5	1750	4	36	100	50	30.4	22.9	25.3	4.7	5.2	0.0
5	1750	4	36	300	30	41.1	26.8	20.0	3.8	1.2	0.0
5	1750	12	12	100	50	31.8	22.0	27.1	5.7	1.7	0.0
5	1750	12	12	300	30	37.3	36.2	17.0	2.9	0.6	0.2
5	1750	12	36	100	30	41.8	25.4	18.1	4.6	2.9	0.0
5	1750	12	36	300	50	31.1	24.6	28.0	4.2	3.3	0.2

[a] WPR=wet prairie, HPR=herbaceous prairie, TRE=tree island, WSA=willow/dense sawgrass, CYP=cypress/pine, MAN=mangrove/mangrove-prairie transition.

For each of the summary outcome measures of annual home range size, distance between annual centers of activity, and distance between consecutive radio-locations, a discrepancy measure (DM) was calculated. First, for each EU, the mean outcome measure was calculated (e.g., mean home range size for 30 deer in the 6th year of the simulation for the i^{th} EU). Then, for each EU and for each summary outcome, the DM was calculated as

$$D(x_i) = \left|P(x_i) - O_i\right|$$

for $i = 1, 2, 3, \ldots, 32$ and where O was the observed summary outcome and $P_i(x)$ was the summary outcome from the i^{th} EU based on the simulation model. On an annual basis, the observed summary statistics for females were mean home range size of 271 ha, mean distance between consecutive centers of 307 m, and mean distance between consecutive locations of 686 m (Section 3.3.1).

For the summary outcome measures of percentage of observations in each habitat, a discrepancy measure (DM) also was calculated. First, for each EU, the mean outcome measure was calculated (e.g., mean percentage of observations in wet prairie for 30 deer in the 6th year of the simulation for the i^{th} EU). The DM for habitat use was calculated for the i^{th} EU as

$$D_i(x) = \sum_{j=1}^{6} \frac{\left(P_{ij}(x) - O_j\right)^2}{O_j}$$

for $i = 1, 2, 3, \ldots, 32$ and where O_j was the mean percentage of time observed deer were radio-located in habitat j and $P_{ij}(x)$ was the mean percentage of time simulated deer were located in habitat j. On an annual basis, the observed summary statistics for females were

50%, 17%, 17%, 9%, 2%, and 2% of radio-locations in wet prairie, herbaceous prairie, tree islands, willow/dense sawgrass, cypress/pine, and mangrove, respectively (Section 3.3.1).

An ANOVA to test for main effects and first-order interactions of the evaluated simulation parameters was performed for each of the four DMs (Table 4.6). Statistical significance was determined using an α-level of 0.05; however, effect size (i.e., relative decrease in the DMs) also was taken into account when determining the most influential factors and the levels to be used in the subsequent simulation experiment.

All average home range sizes of the simulated females were larger than those of females observed in the field. The DM for home range size was significantly smaller with smaller ϕ, smaller μ, larger λ, smaller STEP, and larger $A_{TRE,WSA}$ (see Table 4.3 for factor descriptions). Distance between consecutive annual centers ranged from very close to the observed average to more than three times the observed average. The DM for distance between consecutive centers was reduced with larger ϕ, smaller μ, and a longer ML.

Average distance between consecutive locations ranged from 458 m to 847 m, encompassing the observed value of 686 m. The DM for mean distance between consecutive locations was significantly smaller with smaller μ and larger STEP. Also, there were significant interactions between λ and STEP and between $A_{TRE,WSA}$ and STEP. The interaction between λ and STEP indicated that when STEP=100, an increase in λ caused an increase in the DM and when STEP=300, an increase in λ caused a decrease in the DM. The interaction between $A_{TRE,WSA}$ and STEP indicated that when STEP=100, an increase in $A_{TRE,WSA}$ caused an increase in the DM, and when STEP=300, an increase in $A_{TRE,WSA}$ caused a decrease in the DM.

Table 4.6. Summary of ANOVA results (p-values) from the first calibration experiment for each DM from the 5th year of simulation.

Experiment Factor	Home range size	Annual center shift	5-day distance	Habitat use
ϕ	0.0001	0.0001	0.6471	0.2707
μ	0.0001	0.0030	0.0013	0.8645
λ	0.0020	0.5000	0.1600	0.2588
ML	0.1853	0.0277	0.8252	0.0475
STEP	0.0001	0.0708	0.0001	0.0279
$A_{TRE,WSA}$	0.0014	0.7571	0.4403	0.4109
$\phi * \mu$	0.1642	0.2315	0.1686	0.9795
$\phi * \lambda$	0.2139	0.1823	0.4383	0.3754
$\mu * \lambda$	0.4672	0.3137	0.6073	0.7999
ϕ * ML	0.2764	0.0274	0.8643	0.2044
μ * ML	0.2264	0.6255	0.5227	0.4663
λ * ML	0.3905	0.0568	0.3659	0.9218
ϕ * STEP	0.0739	0.9324	0.1663	0.5359
μ * STEP	0.0008	0.7396	0.0001	0.6528
λ * STEP	0.3346	0.8458	0.0005	0.1028
ML * STEP	0.5827	0.2778	0.7040	0.2202
$\phi * A_{TRE,WSA}$	0.3688	0.5001	0.2724	0.3010
$\mu * A_{TRE,WSA}$	0.4406	0.9300	0.3113	0.3871
$\lambda * A_{TRE,WSA}$	0.8761	0.6816	0.7797	0.8811
ML * $A_{TRE,WSA}$	0.6918	0.6783	0.9174	0.4974
STEP * $A_{TRE,WSA}$	0.0905	0.6761	0.0217	0.9590

Habitat use patterns of the simulated female deer (Table 4.5) were not comparable to those of the observed female deer (Table 3.2). Simulated females were observed in tree islands and herbaceous prairie more and wet prairie less than observed females, indicating a need for further evaluation of relative habitat affinities. An increase in ML and a decrease in STEP caused a decrease in the DM for habitat use. $A_{TRE,WSA}$ and its associated interactions had no significant effect on the DM, perhaps because the overall agreement was poor.

In addition to quantitative analyses of simulation results, qualitative observations also aided in the verification and calibration processes. Movement paths of simulated and observed female deer residing in the same area on the landscape were plotted and compared. For example, during a 1-year interval, one simulated deer had a realistic movement pattern when compared to an observed deer (3-year-old female) in the same geographic area; however, the movement paths of all simulated deer were not similarly realistic, indicating the model still needed improvement (Fig. 4.8).

The outcome measures that had the greatest disagreement with the observed summary data were home range size and habitat use. Analysis results for each summary outcome indicated a direction in the parameter space to move in order to minimize the DM; however, these directions were contradictory for several of the DMs. So, for the subsequent experiment, current parameter settings were maintained. Instead, I focused on minimizing the habitat use discrepancies by including additional factors (e.g., relative affinities for herbaceous prairie, willow/dense sawgrass, cypress, pine, and mangrove) in the following experiment.

4.3.2. Second Calibration Experiment

The second experiment focused on the number of steps over a 5-day interval, parameter values for the home range algorithms, and values for relative habitat affinities (Table 4.7). A 2^{11-6} fractional factorial design was used, which allowed estimation of all main effects with 20 degrees of freedom for experimental error, assuming interactions were negligible. As in the first experiment, each of the 32 EUs consisted of 30 deer, starting in the same locations, simulated for a 15-year time interval. The movement algorithms were not changed from those used in the first calibration experiment.

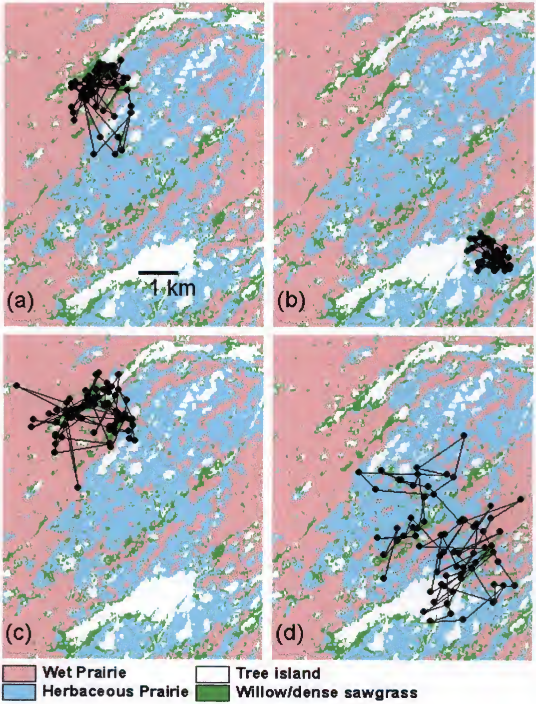

Figure 4.8. Examples of observed and simulated deer movement paths over a 1-year time period. (a) observed adult female; (b) observed adult female; (c) simulated female exhibiting a movement path comparable to the observed females; and (d) simulated female not exhibiting typical site fidelity of observed females.

Table 4.7. Factor levels for second calibration experiment.

Factor description	Symbol	Low	High
Maximum relative affinity for homing beacon	ϕ	3	5
Distance (m) from homing beacon at which affinity is ϕ	μ	750	1750
Relative affinity for previously visited pixels	λ	4	12
Memory length (5-day interval)	ML	12	36
Number of moves per 5-day interval	STEP	100	300
Relative affinity for herbaceous prairie	A_{HPR}	20	30
Relative affinity for tree islands	A_{TRE}	20	50
Relative affinity for willow/dense sawgrass	A_{WSA}	30	50
Relative affinity for cypress	A_{CYS}	5	15
Relative affinity for pine	A_{PIN}	5	15
Relative affinity for mangrove	A_{MAN}	1	10

Annual home range size, distance between consecutive annual centers of activity, mean distance between consecutive locations, and percentage of observations in each habitat were the calculated outcome measures. Using the outcome measures for each of the 15 years of simulation, repeated measures ANOVA was conducted to estimate burn-in time, with a separate analysis for each outcome for each of the 32 EUs. Correlation structures providing the best fit to the data for each outcome were the same as in the first experiment. For distance between consecutive annual centers of activity, mean distance between consecutive locations, and percentage of radio-locations in each of the four major habitats, the auto-correlation structure provided the best fit. For annual home range size, the heterogenous auto-correlation structure provided the best fit. Tests for linear time trends were used to estimate burn-in time for each EU for each outcome. Based on an α-level of 0.01, the maximum burn-in time was estimated at 5 years; thus, summary

data from the 6th year of simulation were used to evaluate the adequacy of the simulation model parameters (Tables 4.8 and 4.9).

DMs were calculated for annual home range size, distance between consecutive radio-locations, distance between annual centers, and habitat use for each of the 32 EUs as in the first experiment. In addition to the four DMs, a mean discrepancy (MD) for each EU was also calculated:

$$\mathrm{MD} = \frac{1}{4}\left[\left(\frac{D_{HR} - \overline{D}_{HR}}{S_{HR}}\right) + \left(\frac{D_{5D} - \overline{D}_{5D}}{S_{5D}}\right) + \left(\frac{D_{CS} - \overline{D}_{CS}}{S_{CS}}\right) + \left(\frac{D_{HU} - \overline{D}_{HU}}{S_{HU}}\right)\right]$$

where D_{HR}, D_{CS}, D_{5D}, and D_{HU} were the discrepancies for home range, annual center shift, 5-day distance, and habitat use (Table 4.9). $\overline{D}_{HR}$, $\overline{D}_{CS}$, $\overline{D}_{5D}$, and $\overline{D}_{HU}$ were the mean discrepancies and S_{HR}, S_{CS}, S_{5D}, and S_{HU} were the standard deviations for home range, annual center shift, 5-day distance, and habitat use discrepancies for this experiment. This measure provided an indication of the factors evaluated in the experiment that had the greatest effect on lack-of-fit of the simulation model output when averaging over all DMs.

An ANOVA testing for main effects of the evaluated simulation parameters was performed for the each of the four DMs and MD using a significance level of 0.05 (Table 4.10). The DM for home range size was significantly smaller with smaller ϕ, smaller μ, larger λ, smaller STEP, and larger A_{TRE} (see Table 4.7 for factor descriptions). The DM for distance between consecutive annual centers was reduced with larger ϕ, smaller μ, longer ML, and larger STEP. The DM for mean distance between consecutive radio-locations was significantly smaller with larger STEP. The DM for habitat use was

Table 4.8. Summary outcomes of home range size, shift in annual centers, distance between consecutive locations, DM for habitat use, and mean discrepancy (MD) from second calibration experiment for adult females for the 6th year of simulation.

ϕ	μ	λ	ML	STEP	A_{HPR}	A_{TRE}	A_{WSA}	A_{CYS}	A_{PIN}	A_{MAN}	Home range size (ha)	Annual center shift (m)	5-day distance (m)	Chi-square	MD
3	750	4	12	100	30	50	50	15	5	1	598	1217	480	40.5	0.32
3	750	4	12	300	20	20	30	5	5	1	893	1025	771	53.9	0.27
3	750	4	36	100	30	50	30	15	15	10	553	660	508	27.7	-0.37
3	750	4	36	300	20	20	50	5	15	10	885	563	822	23.9	-0.25
3	750	12	12	100	20	20	50	15	5	10	541	1378	467	23.4	0.18
3	750	12	12	300	30	50	30	5	5	10	604	861	702	73.3	-0.17
3	750	12	36	100	20	20	30	15	15	1	530	642	511	66.2	0.10
3	750	12	36	300	30	50	50	5	15	1	683	439	777	55.1	-0.32
3	1750	4	12	100	30	20	30	5	15	10	761	1663	507	78.3	1.22
3	1750	4	12	300	20	50	50	15	15	10	1098	1268	810	57.5	0.87
3	1750	4	36	100	30	20	50	5	5	1	799	864	529	29.7	0.00
3	1750	4	36	300	20	50	30	15	5	1	1094	729	846	31.0	0.29
3	1750	12	12	100	20	50	30	5	15	1	641	1539	472	16.9	0.30
3	1750	12	12	300	30	20	50	15	15	1	1107	1379	774	51.2	0.73
3	1750	12	36	100	20	50	50	5	5	10	612	765	499	29.2	-0.18
3	1750	12	36	300	30	20	30	15	5	10	1061	595	836	71.6	0.67
5	750	4	12	100	20	50	50	5	15	1	488	1026	465	19.9	-0.15
5	750	4	12	300	30	20	30	15	15	1	571	662	694	74.8	-0.35
5	750	4	36	100	20	50	30	5	5	10	407	412	489	33.9	-0.55
5	750	4	36	300	30	20	50	15	5	10	568	345	758	62.5	-0.49

Table 4.8. – continued.

ϕ	μ	λ	ML	STEP	A_{HPR}	A_{TRE}	A_{WSA}	A_{CYS}	A_{PIN}	A_{MAN}	Home range size (ha)	Annual center shift (m)	5-day distance (m)	Chi-square	MD
5	750	12	12	100	30	20	50	5	15	10	399	911	461	48.9	0.07
5	750	12	12	300	20	50	30	15	15	10	468	714	667	49.4	-0.74
5	750	12	36	100	30	20	30	5	5	1	394	377	488	66.1	-0.15
5	750	12	36	300	20	50	50	15	5	1	471	288	710	38.4	-1.12
5	1750	4	12	100	20	20	30	15	5	10	730	1551	503	11.9	0.23
5	1750	4	12	300	30	50	50	5	5	10	872	1098	771	42.9	0.15
5	1750	4	36	100	20	20	50	15	15	1	631	817	522	36.7	-0.11
5	1750	4	36	300	30	50	30	5	15	1	879	474	812	51.6	0.01
5	1750	12	12	100	30	50	30	15	5	1	565	968	461	43.6	0.23
5	1750	12	12	300	20	20	50	5	5	1	850	1248	741	26.0	-0.12
5	1750	12	36	100	30	50	50	15	15	10	570	714	512	24.7	-0.37
5	1750	12	36	300	20	20	30	5	15	10	862	532	836	29.3	-0.18

Table 4.9. Summary outcome measures of percentage of observations in each habitat from the second calibration experiment for adult females for the 6th year of simulation.

ϕ	μ	λ	ML	STEP	A_{HPR}	A_{TRE}	A_{WSA}	A_{CYS}	A_{PIN}	A_{MAN}	Percentage of observations in each habitat[a]					
											WPR	HPR	TRE	WSA	CYP	MAN
3	750	4	12	100	30	50	50	15	5	1	24.4	34.4	24.7	5.0	2.6	0.1
3	750	4	12	300	20	20	30	5	5	1	32.8	42.9	13.4	3.5	0.8	0.0
3	750	4	36	100	30	50	30	15	15	10	35.5	27.2	25.3	2.3	5.3	0.3
3	750	4	36	300	20	20	50	5	15	10	34.0	32.1	13.5	5.2	0.4	2.0
3	750	12	12	100	20	20	50	15	5	10	40.7	26.6	10.6	4.4	6.1	0.0
3	750	12	12	300	30	50	30	5	5	10	18.3	38.3	32.6	1.7	0.5	4.2
3	750	12	36	100	20	20	30	15	15	1	42.1	27.0	10.3	2.5	11.9	0.1
3	750	12	36	300	30	50	50	5	15	1	23.5	38.5	26.9	4.4	0.4	0.0
3	1750	4	12	100	30	20	30	5	15	10	31.3	48.9	10.6	2.9	0.3	0.3
3	1750	4	12	300	20	50	50	15	15	10	20.8	27.1	29.2	3.7	8.3	1.3
3	1750	4	36	100	30	20	50	5	5	1	42.7	33.8	6.8	4.7	0.7	0.0
3	1750	4	36	300	20	50	30	15	5	1	31.9	29.4	26.7	2.3	4.1	0.6
3	1750	12	12	100	20	50	30	5	15	1	40.5	23.2	21.9	2.5	5.0	0.5
3	1750	12	12	300	30	20	50	15	15	1	33.8	39.0	9.4	3.3	5.6	0.0
3	1750	12	36	100	20	50	50	5	5	10	29.3	22.4	30.9	3.5	2.0	4.1
3	1750	12	36	300	30	20	30	15	5	10	29.2	44.0	10.2	2.3	6.4	3.1
5	750	4	12	100	20	50	50	5	15	1	36.6	21.9	28.9	4.4	0.4	0.4
5	750	4	12	300	30	20	30	15	15	1	32.4	47.1	8.5	2.2	4.1	0.1
5	750	4	36	100	20	50	30	5	5	10	33.9	26.8	32.2	2.1	0.0	0.9
5	750	4	36	300	30	20	50	15	5	10	28.1	43.8	7.7	4.4	2.8	3.2

Table 4.9. – continued.

ϕ	μ	λ	ML	STEP	A_{HPR}	A_{TRE}	A_{WSA}	A_{CYS}	A_{PIN}	A_{MAN}	Percentage of observations in each habitat					
											WPR	HPR	TRE	WSA	CYP	MAN
5	750	12	12	100	30	20	50	5	15	10	28.6	40.0	12.4	4.9	0.1	3.8
5	750	12	12	300	20	50	30	15	15	10	26.1	18.9	36.2	2.8	5.8	4.1
5	750	12	36	100	30	20	30	5	5	1	35.1	45.9	9.7	3.0	0.1	0.0
5	750	12	36	300	20	50	50	15	5	1	23.9	24.6	32.8	5.3	3.5	0.2
5	1750	4	12	100	20	20	30	15	5	10	46.9	27.0	10.9	4.0	1.5	1.3
5	1750	4	12	300	30	50	50	5	5	10	24.0	30.7	29.6	3.7	0.2	3.9
5	1750	4	36	100	20	20	50	15	15	1	35.1	26.5	13.4	4.9	8.5	0.3
5	1750	4	36	300	30	50	30	5	15	1	26.4	36.3	29.3	2.5	0.2	0.6
5	1750	12	12	100	30	50	30	15	5	1	26.5	34.2	27.5	3.1	0.9	0.0
5	1750	12	12	300	20	20	50	5	5	1	36.9	33.0	14.4	4.4	0.4	0.0
5	1750	12	36	100	30	50	50	15	15	10	34.6	30.8	22.5	2.9	0.5	1.9
5	1750	12	36	300	20	20	30	5	15	10	40.2	35.3	12.6	3.6	0.6	0.5

[a] WPR=wet prairie, HPR=herbaceous prairie, TRE=tree island, WSA=willow/dense sawgrass, CYP=cypress/pine, MAN=mangrove/mangrove-prairie transition.

significantly smaller with smaller A_{HPR}. Overall, habitat use of the simulated deer exhibited strong lack of fit evidenced by the large values of the chi-square DM and the mean percentage of observations of simulated deer in each habitat. Adjustments to relative affinity scores for the subsequent experiment were made based on the mean percentage of radio-locations in each habitat for each of the relative affinities (Table 4.11).

Table 4.10. Summary of ANOVA results (p-values) from the second calibration experiment for each DM and the mean discrepancy for the 6th year of simulation.

Experiment Factor	Home range size	Annual center shift	5-day distance	Habitat use	Mean discrepancy
ϕ	0.0001	0.0001	0.3439	0.4387	0.0001
μ	0.0001	0.0001	0.1761	0.1647	0.0001
λ	0.0024	0.1313	0.7828	0.6787	0.1625
ML	0.6581	0.0001	0.4619	0.6956	0.0005
STEP	0.0001	0.0001	0.0001	0.0367	0.3152
A_{HPR}	0.6133	0.0504	0.5917	0.0029	0.1293
A_{TRE}	0.0309	0.0448	0.9891	0.1876	0.0238
A_{WSA}	0.7129	0.1430	0.8878	0.0661	0.2955
A_{CYS}	0.7703	0.7923	0.5421	0.7149	0.9397
A_{PIN}	0.8733	0.7072	0.8288	0.6987	0.5496
A_{MAN}	0.6354	0.6388	0.7003	0.8825	0.9921

MD was significantly reduced with larger ϕ, smaller μ, and longer ML. MD was also reduced with larger A_{TRE}. This finding was misleading because with larger A_{TRE}, home range sizes had smaller discrepancies; however, concurrently, the percentage of locations of individuals in tree islands was much higher than was observed in the field. When plots of simulated female deer movement paths were reviewed, some individuals

were finding and concentrating their movements in tree islands and not moving into the prairies, indicating a need to reevaluate some of the movement algorithms and parameters.

For the subsequent simulation experiment, ϕ was increased, and A_{HPR}, A_{TRE}, and A_{WSA}, and A_{MAN} were decreased. Because cypress and pine habitats were a minor component of the habitat map and not this focus of the study, A_{CYS} and A_{PIN} were combined as A_{CYP} in future experiments.

Table 4.11. Mean percentage of radio-locations in each habitat for each relative affinity score from the second calibration experiment for the 6th year of simulation.

		Habitat[a]					
Factor	Levels	WPR	HPR	TRE	WSA	CYP	MAN
A_{HPR}	20	34	28	21	4	4	1
	30	30	38	18	3	2	1
A_{TRE}	20	36	37	11	4	3	1
	50	29	29	29	3	2	1
A_{WSA}	30	33	34	20	3	3	1
	50	31	32	20	4	3	1
A_{CYS}	5	32	34	20	4	1	1
	15	32	32	19	4	5	1
A_{PIN}	5	32	34	20	4	2	1
	15	33	33	19	3	4	1
A_{MAN}	1	33	34	19	4	3	0
	10	32	32	20	3	3	2

[a] WPR=wet prairie, HPR=herbaceous prairie, TRE=tree island, WSA=willow/dense sawgrass, CYP=cypress/pine, MAN=mangrove/mangrove-prairie transition.

4.4. Final Movement Model

The model for adult females and for adult males was finalized after calibration with the observed field data through a series of simulation experiments. The final algorithms, parameter values, and factor weights used in the movement decisions were determined through experimentation during the model calibration (Appendices C and D). Several algorithms were changed from the initial description in Section 4.2, so all movement algorithms were described in the following sections for completeness.

Because deer could not move off the map, the habitat map was considered a closed environment. Initial locations of simulated deer were located randomly in the study area at least 1.5 km from the perimeter of the habitat map (Fig. 4.9); however, there was no 'repelling force' to prevent them from moving towards the edge of the map.

Simulated deer made multiple movements over a 5-day interval, the interval over which simulated 'radio-locations' were taken. Each movement was a two-stage process. In the first stage of each movement iteration, the deer moved a maximum of one pixel in any direction, using 60-m pixels (Fig. 4.5). During this stage, the deer evaluated its surroundings and determined the probability of moving to each pixel based on habitat, water depth, and relative location in its home range. The second stage consisted of selecting a 20-m pixel inside the 60-m pixel and was based solely on habitat and water depth. Females made 200 two-stage moves per 5-day interval, and males made 250 two-stage moves per 5-day interval.

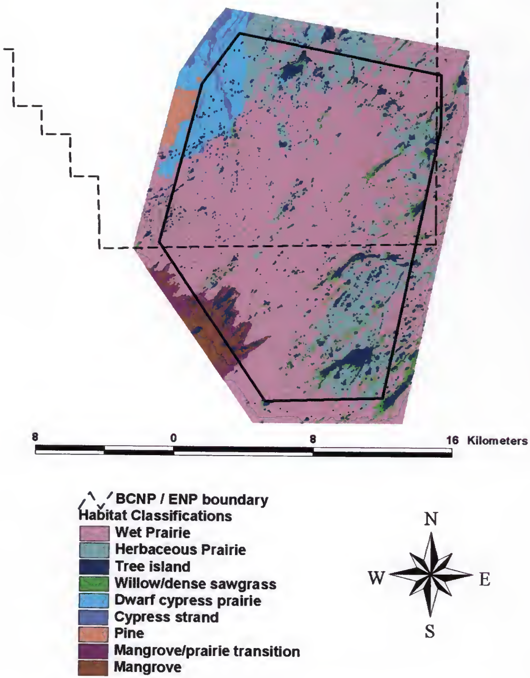

Figure 4.9. Starting locations of simulated deer were located randomly within the solid black line (approximately 1.5 km from edge of habitat map).

4.4.1. 60-m Movement Stage

Each 20-m pixel was assigned a relative affinity score based on habitat contained within the pixel (Table 4.12). A habitat relative affinity score for a 60-m pixel was determined using the mean relative affinity of the nine 20-m pixels contained within it.

Table 4.12. Habitat relative affinity scores for the final simulation model.

Habitat	Relative affinity	
	Female	Male
Wet prairie	10	10
Herbaceous prairie	10	35
Tree island	35	100
Willow/dense sawgrass	40	150
Cypress prairie/strand	7.5	5
Pine	7.5	5
Mangrove	10	5

Water depth in each 60-m pixel was calculated as the mean water depth of the nine 20-m pixels contained within it. A relative affinity score for each 60-m pixel was calculated as

$$affinity_j = \begin{cases} \alpha & \text{if depth} < \beta \\ \alpha - \left[\left(\dfrac{\alpha - 1}{\gamma - \beta}\right)(\text{depth} - \beta)\right] & \text{if } \beta \le \text{depth} \le \gamma \\ 1 & \text{if depth} > \gamma \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$ and where α=20, β=10 cm, and γ=40 cm for females and α=10, β=30 cm, and γ=60 cm for males (see Fig 4.6).

In addition to evaluating habitat and water depth in the current and the adjacent pixels, deer used information on habitat and water depth from pixels in the vicinity of its

current location, but not adjacent to its current location (Fig. 4.10). The simulated deer used the information regarding 'long-distance habitat' and 'long-distance water depth' in these pixels to influence movement to the adjacent pixels.

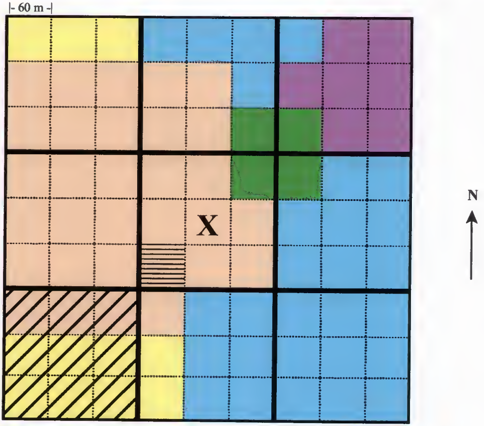

Figure 4.10. Calculation of relative affinities using pixels farther than the pixels adjacent to the current location of a hypothetical deer (center 60-m pixel marked with a large **X**). Each small square is a 60-m pixel, and the colors represent relative affinity scores assigned to each 60-m pixel (based on either habitat or water depth). A deer could move to any of the eight immediately surrounding 60-m pixels or stay in its current pixel. For each of these neighboring pixels, the 'long-distance' relative affinity was the mean affinity of the nine 60-m pixels associated with it. For example, the long-distance relative affinity for the pixel southwest of the current location of the deer (horizontal hatch marks) was the mean affinity score of the nine pixels further southwest (diagonal hatch marks).

The homing beacon algorithm provided simulated deer with an affinity for pixels closer to their homing beacon, $\left(\bar{x}_{\text{home}}, \bar{y}_{\text{home}}\right)$. The location of the homing beacon, based on 24 previous radio-location coordinates, was updated every 5 days using the moving averages:

$$\bar{x}_{\text{home}} = \frac{1}{24}\left(x_t + x_{t-1} + x_{t-2} + \ldots + x_{t-23}\right)$$
$$\bar{y}_{\text{home}} = \frac{1}{24}\left(y_t + y_{t-1} + y_{t-2} + \ldots + y_{t-23}\right)$$

where (x_t, y_t) were coordinates of the most recent radio-location, and (x_{t-1}, y_{t-1}) were coordinates of the radio-location taken 5 days earlier, etc. This window of time used to calculate the location of the homing beacon encompassed the 24 previous radio-locations.

The relative affinity scores for the nine pixels to which the deer could move were based on the direction of travel from the current location of the deer to the homing beacon (Fig. 4.11). The strength of the beacon, δ (equal to 1, ϕ, or ϕ^2), was reduced exponentially as a deer moved closer to its homing beacon:

$$affinity_j = \begin{cases} \delta^{z/\mu} & \text{if } z < \mu \\ \delta & \text{otherwise} \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$, and where δ or $\delta^{z/\mu}$ was the relative affinity score, μ was the distance from homing beacon at which the relative affinity was constant, and z was the distance from current location to homing beacon. For females and males, μ=500 m.

By altering the value of ϕ over the course of an annual cycle, seasonal changes in movement patterns were simulated. For females, ϕ=4 when water depth at P-34 (the gauging station) was >0 cm, and ϕ=3 when water depth at P-34 was <0 cm, enabling

them to travel farther during the dry season to simulate an expanding search for forage. For males, the value of ϕ decreased during rut to simulate the search for females. From November through May, ϕ=3. During June, as males came into the rutting season, ϕ=2.5. During the peak of rut, from July to September, ϕ=2. During October, as the rutting season concluded, ϕ=2.5.

(a)

1	1	1
ϕ	ϕ	ϕ
ϕ	ϕ	ϕ

(b)

1	ϕ	ϕ
1	ϕ	ϕ
1	ϕ	ϕ

(c)

1	ϕ	ϕ
ϕ	ϕ^2	ϕ^2
ϕ	ϕ^2	ϕ^2

N

Figure 4.11. Illustration of homing beacon relative affinity calculations, with the homing beacon located southeast of current location [center pixel of (a), (b), and (c)]. Affinity scores to move (a) towards the south and (b) towards the east are multiplied to give (c) δ (equal to 1, ϕ, ϕ^2) which was used to calculate the relative affinity scores of moving to each of nine possible pixels.

The pixel memory algorithm gave simulated deer a stronger affinity for previously visited pixels than for unfamiliar pixels. Pixels visited in the immediate past were avoided to prevent deer from moving to habitat with a high affinity (e.g., tree island) and not venturing out of that habitat patch. For females, the relative affinity score for pixel j was defined as

$$affinity_j = \begin{cases} 0.5 & \text{visited in previous 40 steps} \\ 5.0 & \text{visited in previous 30 days (but not in previous 40 steps)} \\ 1.0 & \text{not visited in previous 30 days} \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$. For males, the relative affinity score for pixel j was defined as

$$affinity_j = \begin{cases} 0.5 & \text{visited in previous 125 steps} \\ 5.0 & \text{visited in previous 30 days (but not in previous 125 steps)} \\ 1.0 & \text{not visited in previous 30 days} \end{cases}$$

for $j = 1, 2, 3, \ldots, 9$.

The relative affinity scores for each pixel for each of the six factors (i.e., habitat, long-distance habitat, water depth, long-distance water depth, homing beacon, and pixel memory) were standardized by converting them to probabilities:

$$p_{ij} = \frac{affinity_{ij}}{\sum_{j=1}^{9} affinity_{ij}}$$

for $j = 1, 2, 3, \ldots, 9$ and where p_{ij} was the probability of moving to pixel j for factor i and $affinity_{ij}$ was the relative affinity score for pixel j for factor i.

For each of the nine pixels to which the deer could move, the probabilities for moving to a pixel based on habitat (i.e., habitat inside the pixel under consideration and habitat in the nine 'long-distance' pixels) or water depth were combined using a weighted average. For females, the weighted averages for habitat and water depth were

$$p_{\text{habitat}} = \left(0.8 \times p_{\text{adjacent habitat}}\right) + \left(0.2 \times p_{\text{long-distance habitat}}\right)$$
$$p_{\text{water}} = \left(0.8 \times p_{\text{adjacent water}}\right) + \left(0.2 \times p_{\text{long-distance water}}\right)$$

Because males have a stronger affinity for wooded areas than females and tend to travel farther, 'long-distance habitat' and 'long-distance water' were weighted more heavily

when calculating the probability of moving to a given pixel based on habitat or water depth:

$$p_{\text{habitat}} = \left(0.6 \times p_{\text{adjacent habitat}}\right) + \left(0.4 \times p_{\text{long-distance habitat}}\right)$$
$$p_{\text{water}} = \left(0.6 \times p_{\text{adjacent water}}\right) + \left(0.4 \times p_{\text{long-distance water}}\right)$$

During the first 4 months of the simulation, deer initialized their memories for the homing beacon and pixel memory algorithms. The probability of moving to j^{th} ($j = 1, 2, 3, \ldots, 9$) pixel was calculated as

$$\pi_j = \left(0.45 \times p_{\text{habitat}}\right) + \left(0.45 \times p_{\text{water}}\right) + \left(0.10 \times p_{\text{homing beacon}}\right)$$

for females, and as

$$\pi_j = \left(0.45 \times p_{\text{habitat}}\right) + \left(0.45 \times p_{\text{water}}\right) + \left(0.05 \times p_{\text{homing beacon}}\right) + \left(0.05 \times p_{\text{pixel memory}}\right)$$

for males. Throughout the remainder of the simulation the probability of moving to the j^{th} ($j = 1, 2, 3, \ldots, 9$) pixel was calculated as

$$\pi_j = \left(0.25 \times p_{\text{habitat}}\right) + \left(0.25 \times p_{\text{water}}\right) + \left(0.25 \times p_{\text{homing beacon}}\right) + \left(0.25 \times p_{\text{pixel memory}}\right)$$

for females. For males, the weights of the four factors depended on biological season. For most of the year, the four factors were weighted as

$$\pi_j = \left(0.35 \times p_{\text{habitat}}\right) + \left(0.15 \times p_{\text{water}}\right) + \left(0.25 \times p_{\text{homing beacon}}\right) + \left(0.25 \times p_{\text{pixel memory}}\right)$$

However, during rut (July, August, and September), simulated males had a reduced weighting of habitat and an increased weighting of pixel memory on their movement

decisions; therefore, the four factors were weighted as

$$\pi_j = \left(0.23 \times p_{\text{habitat}}\right) + \left(0.12 \times p_{\text{water}}\right) + \left(0.25 \times p_{\text{homing beacon}}\right) + \left(0.40 \times p_{\text{pixel memory}}\right)$$

Each deer chose a 60-m pixel for its next location based on a random draw from the multinomial distribution ($\pi_1, \pi_2, \pi_3, \ldots, \pi_9$).

4.4.2. 20-m Movement Stage

The nine 20-m pixels contained inside the 60-m pixel were evaluated based on habitat and water depth. For females and males, probabilities of moving to each 20-m pixel were calculated from relative affinity scores for habitat and water depth, and the probabilities of moving to each pixel were calculated as

$$\pi'_j = \frac{1}{2}\left(p'_{1j} + p'_{2j}\right)$$

where p'_{1j} and p'_{2j} were the probabilities of moving to the j^{th} 20-m pixel based on habitat and water depth, respectively. The deer selected a 20-m pixel based on a random draw from the multinomial distribution ($\pi'_1, \pi'_2, \pi'_3, \ldots, \pi'_9$).

4.5. Evaluation Approach for the Final Movement Model

To evaluate performance of the final model, 50 runs of the simulation for females and 50 runs of the simulation for males (each consisting of 30 individuals) were conducted using the final model parameterization detailed in Section 4.4. Analyses of the final models were done separately for each gender.

For burn-in evaluation, the annual outcome measures of home range size, distance between consecutive home range centers, mean distance between consecutive locations, and percentage of locations in each of the four major habitats (wet prairie, herbaceous

prairie, tree islands, and willow/dense sawgrass) were used. For each run of the simulation, burn-in time was estimated, and based on these results, a burn-in time for the simulation model was determined.

Once burn-in time was established for the final model, performance was evaluated using data from the 1st year after completion of simulation burn-in. The mean annual outcome measures of home range size, distance between consecutive home range centers, mean distance between consecutive locations, and percentage of locations in each of the habitats (wet prairie, herbaceous prairie, tree islands, willow/dense sawgrass, cypress/pine, and mangrove) from the simulation were compared to the observed mean annual outcome measures from the field data. Also, comparisons were made on a hydrologic season basis, using the seasonal outcomes of home range size, distance between consecutive locations, and percentage of locations in each of the four major habitats (wet prairie, herbaceous prairie, tree islands, and willow/dense sawgrass). Simulated deer that were radio-located in the cypress/pine or mangrove habitats were not included in calculation of mean percentage of locations in the four major habitats. These comparisons were performed using a predictive p-value analysis (Section 4.1.6) in which the likelihood of the value of the observed outcome (i.e., mean from the field data) arising as an outcome of the simulation was assessed.

4.6. Evaluation of the Final Movement Model for Females

Variability in outcome measures was high both among individuals (Figs. 4.12 and 4.13) and among simulation runs (Figs. 4.14 and 4.15). However, the variation in outcomes was much larger among individuals within a simulation than among means for each simulation run. Because of heterogeneity in habitat across the study site, a simulated

deer placed in one area of the map may have different habitat-use patterns than a deer placed several kilometers away. The impact of habitat heterogeneity on the variance of the outcome measures was minimized as the number of simulation runs increased.

Of the 50 simulation runs, 56% required no burn-in period (i.e., no significant linear trend over time), 24% had a burn-in time of 1 year, 10% had a burn-in time of 2 years, 6% had a burn-in time of 3 years, and 4% had a burn-in time of >4 years. Based on these results, data from the 4th year of simulation were used to evaluate the final model.

Home range size and distance between consecutive measurements initially decreased from the 1st year to the 2nd year and then stabilized for the remainder of the simulation. This was due primarily to the fact that the home range algorithms had less weight in the movement decision during the first 4 months of the simulation then they did during the rest of the simulation run. The outcome measures that required the most time to stabilize were the percentages of observations in wet prairie and in tree islands. On average, percentage of observations in the tree islands tended to increase and percentage of observations in wet prairie tended to decrease for the first several years of the simulation. This trend was not present in all runs of the simulation (e.g., the simulation run depicted in Fig. 4.12 and 4.13). For this randomly selected run, several individual deer showed an increase in percentage of observations in tree islands, and one showed an increase in percentage of locations in the herbaceous prairie; but most deer appeared to exhibit consistent habitat-use patterns over time. For this particular experimental run, there was no significant linear trend over time (i.e., no burn-in period) for any of the outcome measures.

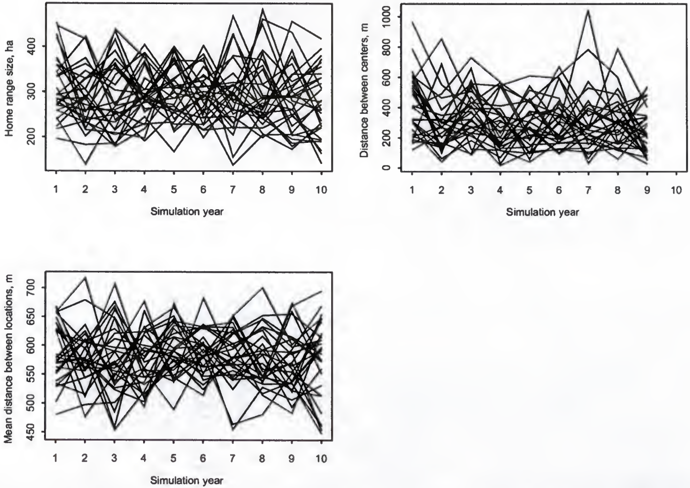

Figure 4.12. Time trend for *annual* home range size, distance between consecutive home range centers, and distance between consecutive locations for 30 simulated female deer. Each line represents one deer within a single simulation run.

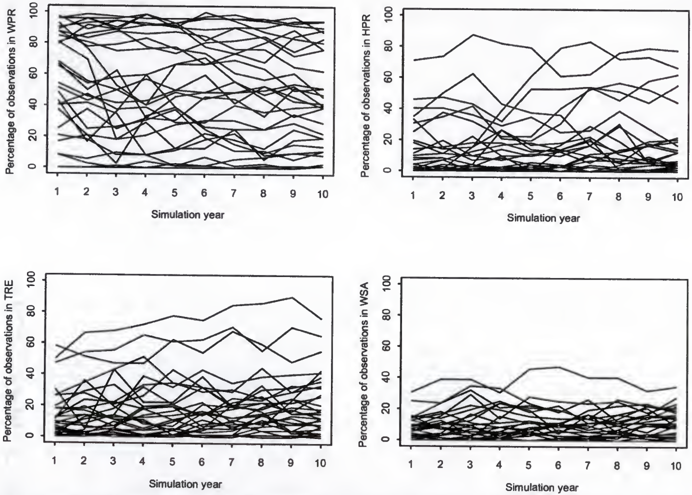

Figure 4.13. Time trend for *annual* percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) for 30 simulated female deer. Each line represents one deer within a single run.

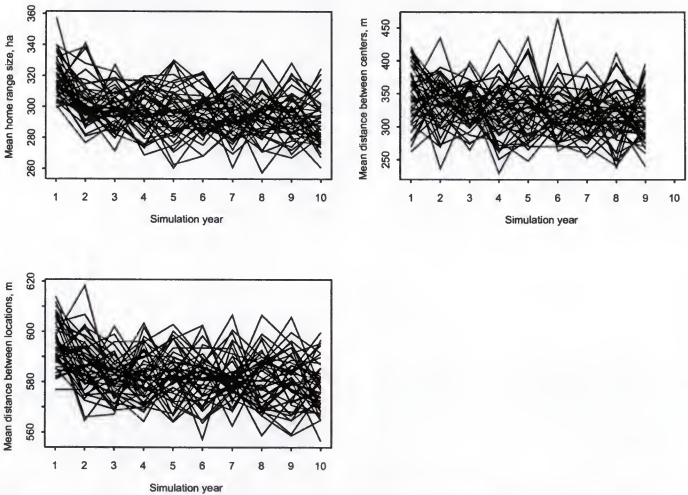

Figure 4.14. Time trend from 50 simulation runs (each with 30 females) for *annual* home range size, distance between consecutive home range centers, and distance between consecutive locations. Each line represents mean outcomes for one run.

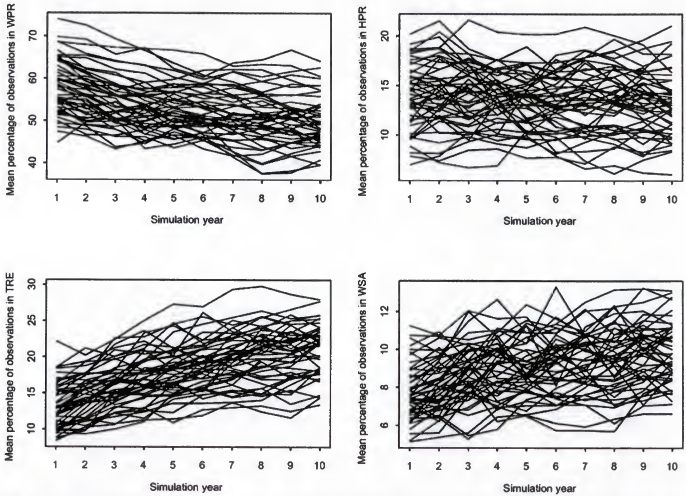

Figure 4.15. Time trend from 50 simulation runs (each with 30 females) for *annual* percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree island (TRE), and willow/sawgrass (WSA). Each line represents means for one run.

Having established burn-in time for the final model, the performance of the model was evaluated (Table 4.13). Using data from the 4th simulation year, predictive p-values were calculated to evaluate the likelihood of the values of the observed outcomes arising as realizations of the final simulation model (Table 4.14). Additionally, histograms of the summary outcomes were plotted with the observed field data means (Figs. 4.16, 4.17, and 4.18).

Annual home range sizes from the simulation tended to be slightly larger than the observed mean home range size by 25 to 50 ha. Distance between annual home range centers from the simulations compared favorably with the observed mean distance between home range centers. Mean distance between consecutive locations from the simulations tended to be smaller than the observed mean distance between consecutive locations by approximately 100 m. Habitat use (represented by mean percentage of observations in the six habitats) also was comparable to the observed field data, and the predictive p-values indicated a high likelihood that the values of the observed mean percentages could have arisen from the simulation model.

On a hydrologic season basis, there was an increase in home range size and mean distance between consecutive locations from the wet to the dry seasons, as observed in the field data; however, the seasonal shift was not as large as expected. Habitat use, based on percentage of observations in each habitat, was similar to that seen in the observed data. Observed females did not exhibit any significant shift in habitat use seasonally, and the simulated data followed this pattern also.

Based on the predictive p-value analysis, the simulation model performed well for all the outcome measures except for home range size and mean distance between consecutive locations. Average home ranges sizes produced by the simulation model were comparable to those observed in the field during the dry season, and simulated deer had smaller home ranges during the wet season. However, the shift in home range size from the dry to the wet season was not as large as expected based on the observed field data. This reduced size of the seasonal shift probably impacted the annual home range sizes as well, leading to larger then expected home range sizes. However, the size of these discrepancies was relatively small (<50 ha).

The discrepancy in mean distance between consecutive locations between the observed and simulated deer was much larger. However, this model lack-of-fit was not of great concern for two reasons. First, this measure had no biological meaning. Straight-line distance between two consecutive radio-locations was used principally as an indicator of the minimum distance a deer traveled over a 5-day interval. Second, the distribution of the straight-line distance between two consecutive radio-locations of the observed deer was extremely skewed to the right (Fig. 3.2). A more appropriate measure of central tendency may have been the median, instead of the mean. To evaluate this hypothesis, the median distance between two consecutive radio-locations was calculated for each observed deer for each of the annual cycles and for each of the hydrologic seasons. The new outcome measure for the field data was the weighted average of the median distances. Average median distances were also calculated for each of the 50 simulation runs for the annual cycle and for the wet and dry hydrologic seasons in the 4th year of the simulation. For the calibration data, the average median distance between two

Table 4.13. Mean outcome measures from the 4th year of 50 simulation runs (each with 30 females) using the final parameterization of the simulation model.

Outcome measure	Annual		Wet season		Dry season	
Home range size, ha	298	(2)[a]	269	(2)	307	(2)
Distance between consecutive centers, m	323	(6)	-[b]		-	
Distance between consecutive locations, m	582	(1)	570	(2)	595	(2)
Percentage of observations in each habitat						
Wet prairie	53	(0.8)	59	(0.8)	60	(0.8)
Herbaceous prairie	14	(0.4)	15	(0.5)	14	(0.4)
Tree islands	17	(0.5)	16	(0.5)	16	(0.5)
Willow/dense sawgrass	9	(0.2)	10	(0.3)	11	(0.3)
Cypress/pine	5	(0.3)	-		-	
Mangrove	2	(0.2)	-		-	

[a] Standard error in parentheses.
[b] Outcome measure not evaluated for wet and dry hydrologic seasons.

Table 4.14. Predictive p-values from the 4th year of 50 simulation runs (each with 30 females) using the final parameterization of the simulation model.

Outcome measure	Annual	Wet season	Dry season
Home range size, ha	0.02	0.00	0.48
Distance between consecutive centers, m	0.34	-[a]	-
Distance between consecutive locations, m	0.00	0.00	0.00
Percentage of observations in each habitat			
Wet prairie	0.50	0.32	0.28
Herbaceous prairie	0.08	0.18	0.28
Tree islands	0.48	0.44	0.28
Willow/dense sawgrass	0.44	0.28	0.30
Cypress/pine	0.34	-	-
Mangrove	0.50	-	-

[a] Outcome measure not evaluated for wet and dry hydrologic seasons.

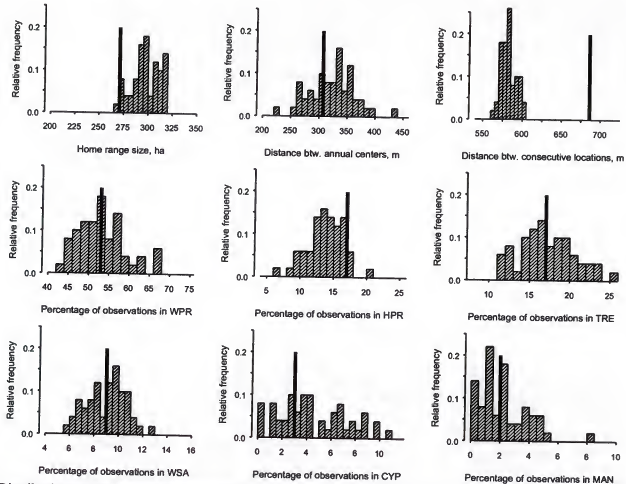

Figure 4.16. Distributions of mean *annual* summary outcomes from 50 runs (each with 30 females) of the final simulation model. Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR=wet prairie, HPR=herbaceous prairie, TRE=tree island, WSA=willow/dense sawgrass, CYP=cypress prairie/cypress swamp/pine, MAN=mangrove.

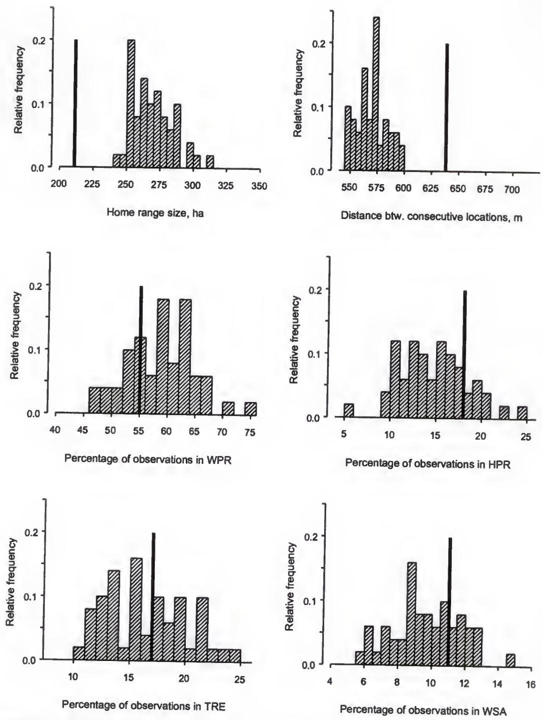

Figure 4.17. Distributions of mean *wet hydrologic season* summary outcomes from 50 runs (each with 30 females) of the final simulation model. Heavy vertical line represents the mean wet hydrologic season summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

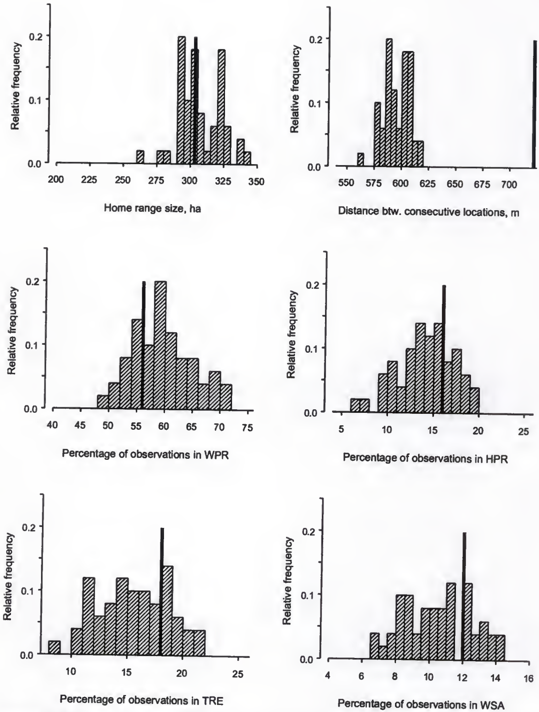

Figure 4.18. Distributions of mean *dry hydrologic season* summary outcomes from 50 runs (each with 30 females) of the final simulation model. Heavy vertical line represents the mean dry hydrologic season summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

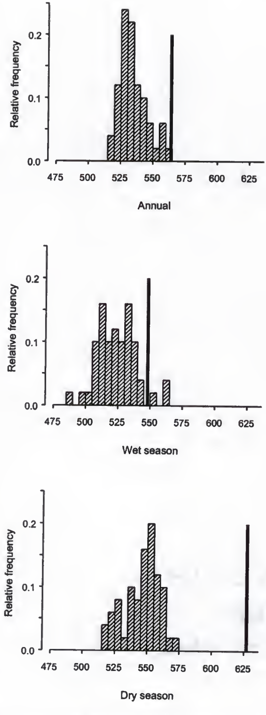

Figure 4.19. Distributions of average median straight-line distance between consecutive radio-locations from 50 runs (each with 30 females) of the final simulation model. Heavy vertical line represents the average median straight-line distance between consecutive radio-locations from the annual cycle, wet hydrologic season, and dry hydrologic season from the calibration data.

consecutive locations was 564 m (se=23) for the annual cycle, 548 m (se=24) for the wet season, and 627 m (se=34) for the dry season. For the simulation data, the average median distance between two consecutive locations was 534 m (se=2) for the annual cycle, 523 m (se=2) for the wet season, and 546 m (se=2) for the dry season. The predictive p-values for the median distances were 0.00 for the annual cycle, 0.06 for the wet season, and 0.00 for the dry season (Fig. 4.19). These predictive p-values still indicated the likelihood of the values of the observed summary outcomes arising as realizations of the simulation model was still small, with respect to median distances between consecutive locations. However, the discrepancy between the observed and simulated outcomes was much smaller (<50 m) than it was using the mean distance between consecutive locations (>100 m). In retrospect, the median would have been a better measure of central tendency for comparison between the observed and simulated data.

4.7. Evaluation of the Final Movement Model for Males

To evaluate the performance of the final model, 50 runs of the simulation for males were conducted using the final model parameterization detailed in Section 4.4. The annual outcome measures that were evaluated included home range size, distance between consecutive home range centers, mean distance between consecutive locations, and percentage of locations in each of the four major habitats (wet prairie, herbaceous prairie, tree islands, and willow/dense sawgrass). Again, the variability in outcome measures was higher among individuals (Figs. 4.20 and 4.21) than it was among simulation runs (Figs. 4.22 and 4.23).

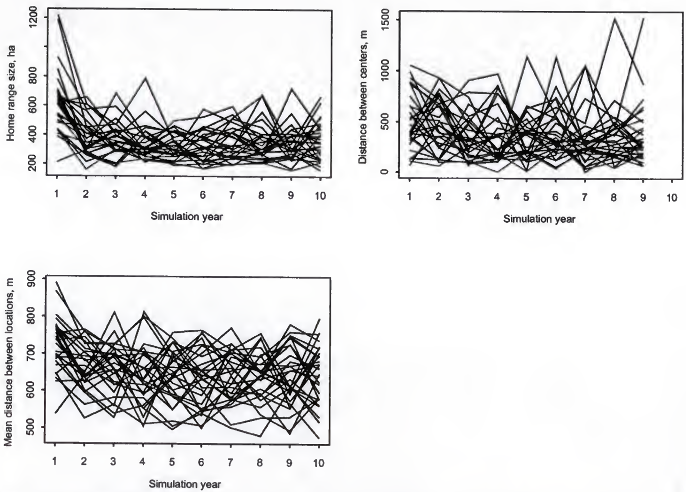

Figure 4.20. Time trend for *annual* home range size, distance between consecutive home range centers, and distance between consecutive locations for 30 simulated male deer. Each line represents one deer within a single simulation run.

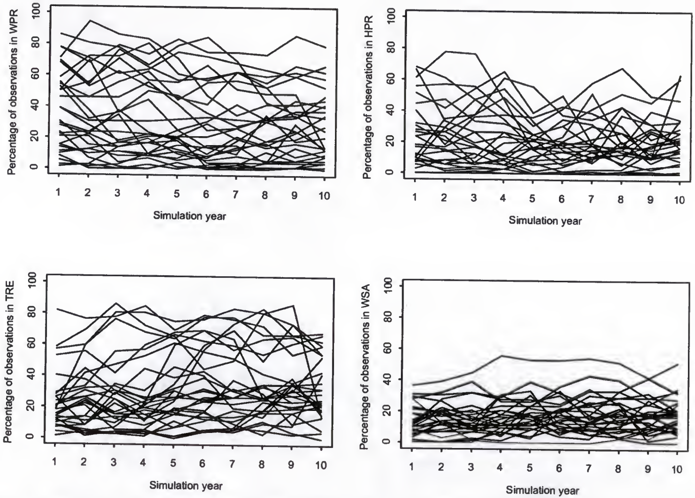

Figure 4.21. Time trend for *annual* percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) for 30 simulated male deer. Each line represents one deer within a single run.

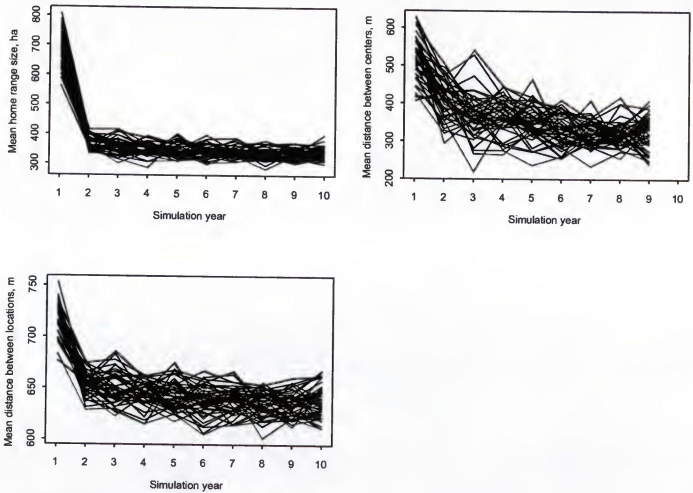

Figure 4.22. Time trend from 50 simulation runs (each with 30 males) for *annual* home range size, distance between consecutive home range centers, and distance between consecutive locations. Each line represents mean outcomes for one run.

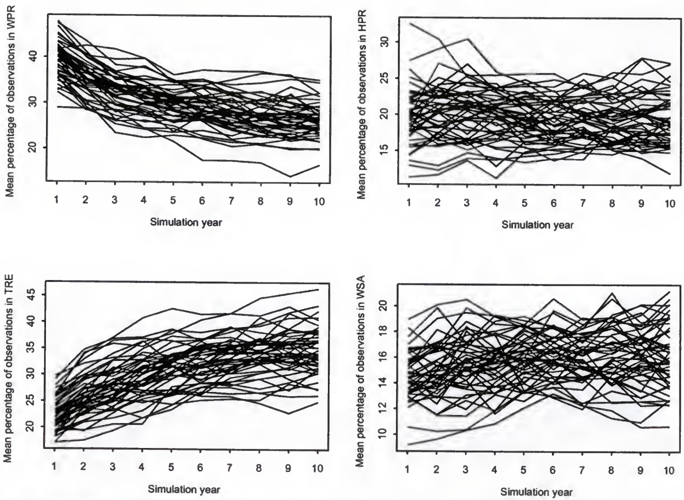

Figure 4.23. Time trend from 50 simulation runs (each with 30 males) for *annual* percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/sawgrass (WSA). Each line represents means for one run.

For each run of the simulation, burn-in time was established. Of the 50 simulation runs, all required at least 1 year to reach a steady state. Forty-four percent had a burn-in time of 1 year, 24% had a burn-in time of 2 years, 20% had a burn-in time of 3 years, 8% had a burn-in time of 4 years, and 4% had a burn-in time of ≥5 years. Further examination of the runs that had long burn-in times indicated that the rate of change of the outcome measure (i.e., the linear regression slope) was small even though it was statistically significant. Based on these results, data from the 4th year of simulation were used to evaluate the final model.

Home range size and distance between consecutive measurements demonstrated an initial decrease from the 1st year to the 2nd year and then stabilized, which was due primarily to the fact that the home range algorithms were weighted lightly for the first several months of the simulation. However, the decrease was more drastic than the decrease observed in the female simulation runs (Fig. 4.14). For the first several years of the simulation, percentage of observations in wet prairie decreased and percentage of observations in tree islands increased. This trend was not present for all deer (e.g., the simulation run depicted in Fig. 4.20 and 4.21). For this randomly selected run, most deer showed a decrease in home range size and average distance between two consecutive locations from the 1st to the 2nd year of the simulation. Although not as evident in the plot, there was also a decrease in the distance between consecutive centers from the 1st to the 2nd year of the simulation. For this simulation run, the burn-in time for each of these three outcomes was 1 year. For this same simulation run, individual deer showed changes in habitat use (i.e., percentage of locations in each habitat) over the 10-year simulation;

however, the averages were consistent over time as there was no significant linear trend over time (i.e., no burn-in time).

The performance of the model was evaluated using data from the 4^{th} year of simulation (Table 4.15). Predictive p-values were calculated to evaluate the likelihood of the values of the observed summary outcomes (i.e., means from the field data) arising as realizations of the final simulation model (Table 4.16). Additionally, histograms of the summary outcomes were plotted with the observed field data (Figs. 4.24, 4.25, and 4.26).

Annual home range sizes and distance between annual home range centers from the simulations for males were slightly greater than the observed outcome measure. Mean distance between consecutive locations from the simulations tended to be less than the observed mean distance between consecutive locations by approximately 150 m. Habitat use (represented by mean percentage of observations in each of the six habitats) was comparable to the observed field data, and the predictive p-values indicated a high likelihood that the values of the observed percentages could have arisen from the simulation model.

The simulation model for males consistently resulted in home ranges sizes and distances between annual home range centers that were greater than expected based on the observed data. If the model was parameterized so that males had smaller home ranges and a shorter distances between annual centers, then several other outcomes were adversely affected. Habitat-use patterns shifted to a heavier use of tree islands and willow/dense sawgrass. Because of restrictions on home range size and the strong affinity for wooded habitat, males would tend to focus their movements in those areas, with little incentive to move into the prairies. As a result, movement patterns of simulated males

Table 4.15. Mean outcome measures from the 4th year of 50 simulation runs (each with 30 males) using the final parameterization of the simulation model.

Outcome measure	Annual		Wet season		Dry season	
Home range size, ha	351	(3)[a]	414	(5)	270	(3)
Distance between consecutive centers, m	365	(6)	-[b]		-	
Distance between consecutive locations, m	645	(2)	696	(2)	593	(2)
Percentage of observations in each habitat						
Wet prairie	31	(0.5)	37	(0.6)	32	(0.6)
Herbaceous prairie	20	(0.5)	22	(0.5)	21	(0.5)
Tree islands	30	(0.6)	25	(0.5)	29	(0.6)
Willow/dense sawgrass	16	(0.3)	16	(0.3)	18	(0.4)
Cypress/pine	2	(0.1)	-		-	
Mangrove	2	(0.2)	-		-	

[a] Standard error in parentheses.

[b] Outcome measure not evaluated for wet and dry hydrologic seasons.

Table 4.16. Predictive p-values from the 4th year of 50 simulation runs (each with 30 males) using the final parameterization of the simulation model.

Outcome measure	Annual	Wet season	Dry season
Home range size, ha	0.06	0.00	0.00
Distance between consecutive centers, m	0.00	-[a]	-
Distance between consecutive locations, m	0.00	0.00	0.00
Percentage of observations in each habitat			
Wet prairie	0.08	0.02	0.00
Herbaceous prairie	0.44	0.30	0.28
Tree islands	0.18	0.00	0.00
Willow/dense sawgrass	0.12	0.38	0.08
Cypress/pine	0.08	-	-
Mangrove	0.28	-	-

[a] Outcome measure not evaluated for wet and dry hydrologic seasons.

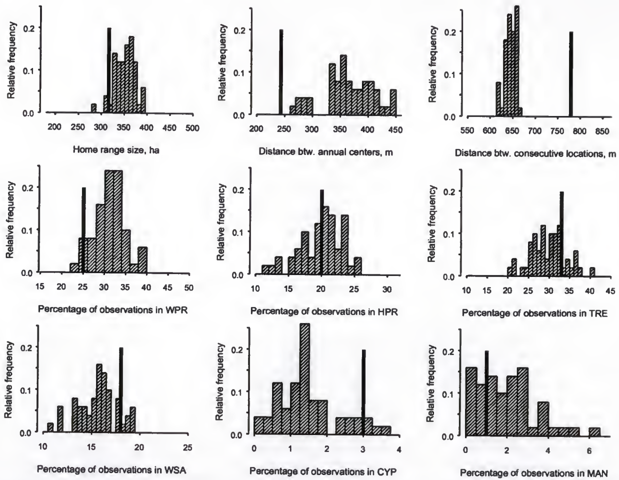

Figure 4.24. Distributions of mean *annual* summary outcomes from 50 runs (each with 30 males) of the final simulation model. Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR=wet prairie, HPR=herbaceous prairie, TRE=tree island, WSA=willow/dense sawgrass, CYP=cypress prairie/cypress swamp/pine, MAN=mangrove.

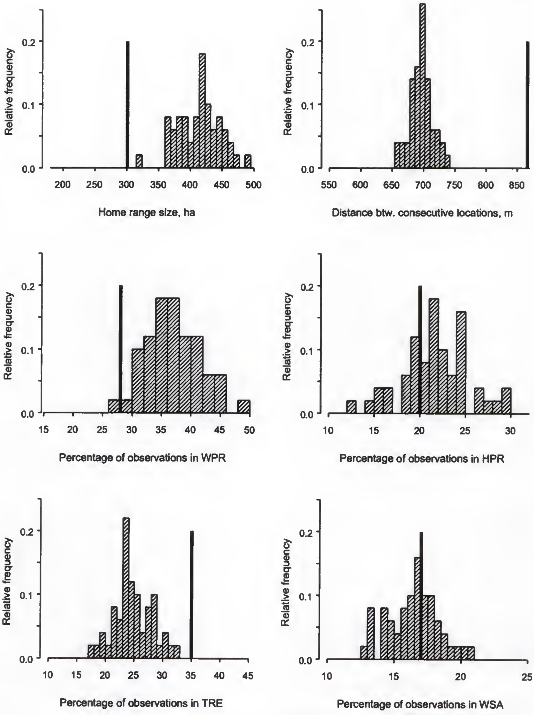

Figure 4.25. Distributions of mean *wet hydrologic season* summary outcomes from 50 runs (each with 30 males) of the final simulation model. Heavy vertical line represents the mean wet hydrologic season summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

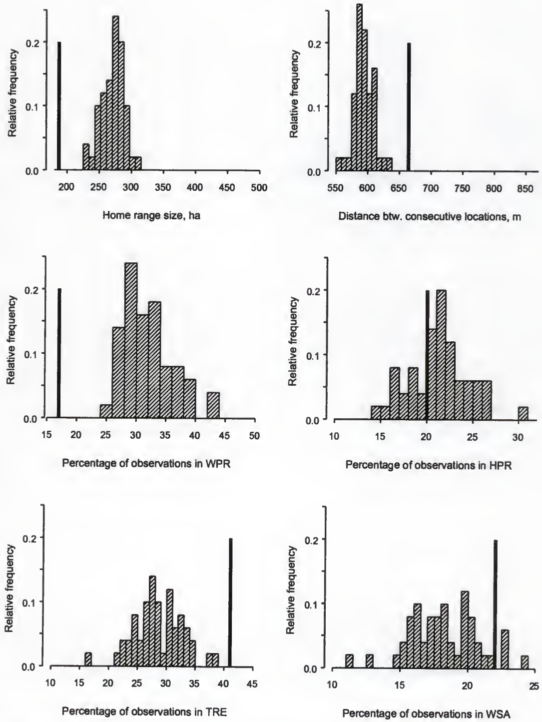

Figure 4.26. Distributions of mean *dry hydrologic season* summary outcomes from 50 runs (each with 30 males) of the final simulation model. Heavy vertical line represents the mean dry hydrologic season summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

would become increasingly focused on wooded areas, and establishing a steady-state would become more difficult. I concluded that a simulation resulting in home ranges and distances between home range centers slightly greater than observed in the field was acceptable, given the alternative of producing simulations with increased burn-in time or simulations that never reached a steady-state.

As with the simulation results for females, distance between consecutive locations for males was less than expected (by >100 m). Again, this measure had little biological meaning, and in retrospect, the average median distance was the better measure. For the calibration data, the average median distance between two consecutive locations for males was 586 m (se=54) for the annual cycle, 761 m (se=67) for the wet season, and 533 m (se=61) for the dry season. For the 50 final simulation runs, the average median distance between two consecutive locations was 581 m (se=2) for the annual cycle, 631 m (se=2) for the wet season, and 540 m (se=2) for the dry season. The predictive p-values for the median distances were 0.34 for the annual cycle, 0.00 for the wet season, and 0.32 for the dry season. With respect to average median distance between consecutive locations, the likelihood of the values of this observed summary outcome arising as realizations of the simulation model was reasonable for the annual cycle and the dry season. The model still underpredicted distances between consecutive locations using medians for the wet season, but the discrepancy was much smaller than when using means.

Based on the observed data, the decrease in home range size from the wet season to the dry season was the same magnitude as expected; however, as discussed previously, the size of the home ranges was larger than expected. Mean distance between consecutive

locations also decreased from the wet season to the dry season, as observed in the field data; however, the seasonal shifts were not as large as expected and the means were smaller than expected. Seasonal habitat-use patterns generally followed those expected based on the observed data. Relative to the wet season, simulated males increased their use of the wooded areas and decreased their use of the wet prairie during the dry season. Seasonal shifts in habitat use of the simulated deer were not as great as those of the observed deer. Overall, on a seasonal basis, simulated deer were observed more frequently in the prairie and less in the wooded areas than expected.

CHAPTER 5
WHITE-TAILED DEER MODEL VALIDATION DATA

The same population of white-tailed deer on the boundary of BCNP/ENP also was studied from 1993-1995 (Labisky et al. 1997, MacDonald 1997). The data collected during this latter study were used to validate and test the simulation model developed in Chapter 4. In August 1992, prior to data collection, Hurricane Andrew moved through the study area and caused extensive damage to tree islands. During the collection of the validation data, environmental conditions ranged from typical to an extreme, extended flood (Fig. 5.1). The fall of 1994 was extremely wet, with >100 cm of rain occurring between August and November, culminating with Tropical Storm Gordon in November 1994, which contributed >20 cm of rain. Water levels remained high throughout 1995.

5.1. Data Collection and Summary Methods

White-tailed deer for this study were captured and monitored using the same techniques as described for the calibration data collection (Section 3.1). A deer was classified as a resident of either BCNP or ENP if ≥75% of its radio-locations were in one of the management units.

For the validation data set, data were collected for two annual cycles [1993 (1 September 1993-31 August 1994) and 1994 (1 September 1994-31 August 1995)]. Deer included in an annual cycle were required to have a minimum of 50 radio-locations and be monitored for a minimum of 9 months during that annual cycle.

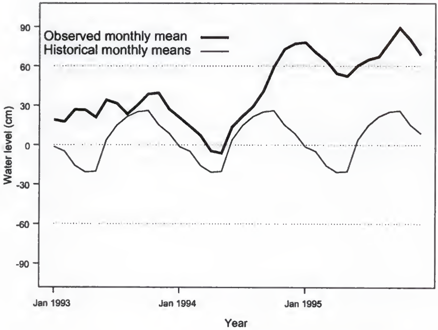

Figure 5.1. Mean monthly water levels recorded at P-34 hydrologic station, and historical monthly mean from 1953-1985. Depths were predicted for January 1993 and February 1993.

Differences in the measured parameters between hydrologic seasons also were estimated. Sufficient radio-telemetry data were collected for 3 hydrologic seasons [93DRY (1 November 1993 - 30 April 1994), 94WET (1 May 1994 - 31 October 1994), and 94DRY(FLOOD) (1 November 1994 - 30 April 1995)]. Each included deer was required to have a minimum of 30 radio-locations and be monitored for a minimum of 5 months in each hydrologic season.

Annual home range size and seasonal home range size were calculated using the 95% fixed kernel estimator with least squares cross validation (Silverman 1986, Worton 1989, Seaman and Powell 1996). Differences between the 2 annual cycles and among the 3 hydrologic seasons were tested using mixed model analyses with deer as a random

effect and either year or hydrologic season as a fixed effect. Separate summary statistics were calculated and separate analyses were performed for females and males.

Resource selection was evaluated for each of the 2 annual cycles and each of the 3 hydrologic seasons using chi-square analyses (Neu et al. 1974, Manly et al. 1993) for design II and design III studies. The details of these statistical methods were described in Section 3.2.1.

5.2. Data Summary

The data set used for model validation included 36 adult deer that were captured, radio-collared, and monitored between 1993 and 1995 (Appendix E). Twenty-seven deer were radio-monitored for 1 year and 9 deer for 2 years. Eight deer were radio-monitored for 1 hydrologic season, 18 deer for 2 seasons, and 10 deer for 3 seasons.

5.2.1. Home Range Size

Home range sizes for females in 1993 (281 ha, se=38, n=19) did not differ (p=0.2021) from home range sizes for females in 1994 (312 ha, se=44, n=10). For males, home range sizes in 1993 (248 ha, se=33, n=9) did not differ (p=0.4914) from home range sizes in 1994 (302 ha, se=41, n=6). Also, there were no significant changes over time when home range size was evaluated on a hydrologic season basis for females (p=0.2656) or males (p=0.3092). Female mean home range size was 265 ha (se=42, n=19) in 93DRY, 301 ha (se=59, n=18) in 94WET, and 176 ha (se=28, n=11) in 94DRY(FLOOD). Male mean home range size was 166 ha (se=23, n=9) in 93DRY, 217 ha (se=34, n=7) in 94WET, and 160 ha (se=31, n=6) in 94DRY(FLOOD).

5.2.3. Habitat Use

Female habitat-use patterns, based on a simple summary of percentage of occurrences in each habitat, appeared to be more strongly affected by the flood conditions than male habitat-use patterns (Tables 5.1 and 5.2). During the preflood year (1993), females were observed most frequently in the wet prairie; however, during the flood year (1994), females used wet prairies less and tree islands more. This same shift in habitat use also was observed across hydrologic seasons. Female habitat-use appeared to be unchanged from 93DRY to 94WET; however, the percentage of observations of females in tree islands increased substantially during 94DRY(FLOOD). For males, the percentage of observations in each habitat changed very little from 1993 to 1994. Based on percentage of radio-locations in each habitat, little shift in male habitat use was evident between 93DRY and 94DRY(FLOOD); however, males were observed in the tree islands less and in the wet prairies more during 94WET than during 93DRY or 94DRY(FLOOD).

Based on the selection ratios, similar changes in habitat-use patterns were observed. Assuming equal availability of habitat for all individuals, females and males exhibited no significant selection for or against any habitat based on the choice of a home range (100% MCP) in 1993 and exhibited only moderate selection for specific habitats in 1994 (Table 5.3). Similarly, on a hydrologic season basis, females and males exhibited no significant selection for or against any habitat based on the choice of a home range (100% MCP) in 93DRY or 94WET and exhibited only moderate selection for specific habitat in 94DRY(FLOOD) (Table 5.4).

Table 5.1. Mean percentage of radio-locations in each habitat for annual cycles for white-tailed deer in BCNP and ENP, September 1993 to August 1995.

	1993[a]		1994	
Female				
Wet prairie	59	(6)[b]	30	(5)
Herbaceous prairie	14	(3)	20	(5)
Tree island	17	(3)	38	(5)
Willow/dense sawgrass	11	(2)	10	(1)
Dwarf cypress prairie	<1	(<1)	1	(1)
Cypress strand	0		<1	(<1)
Male				
Wet prairie	21	(5)	15	(3)
Herbaceous prairie	19	(7)	23	(6)
Tree island	47	(7)	49	(8)
Willow/dense sawgrass	14	(2)	13	(3)
Dwarf cypress prairie	0		0	
Cypress strand	0		0	

[a] Sample sizes: female-1993 (20); female-1994 (10); male-1993 (9); male-1994 (6).
[b] Standard error in parentheses.

Table 5.2. Mean percentage of radio-locations in each habitat for each hydrologic season for white-tailed deer in BCNP and ENP, November 1993 to April 1995.

	93DRY[a]		94WET		94DRY(FLOOD)	
Female						
Wet prairie	58	(6)[b]	59	(6)	16	(7)
Herbaceous prairie	13	(3)	13	(3)	19	(4)
Tree island	18	(4)	18	(3)	57	(6)
Willow/dense sawgrass	11	(2)	10	(2)	9	(2)
Male						
Wet prairie	15	(4)	29	(8)	9	(2)
Herbaceous prairie	20	(8)	18	(4)	20	(7)
Tree island	51	(8)	37	(7)	59	(8)
Willow/dense sawgrass	15	(2)	16	(3)	12	(4)

[a] Sample sizes: female-93DRY (19); female-94WET (18); female-94DRY (10); male-93DRY (9); male-94WET (8); male-94DRY (6).
[b] Standard error in parentheses.

Table 5.3. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for habitat inside 100% MCP for each annual cycle for white-tailed deer in BCNP and ENP, September 1993 to August 1995.

	1993[b]		1994	
Female				
WPR[c]	1.02	(0.85,1.19)	0.59	(0.29,0.90)
HPR	0.90	(0.38,1.43)	2.16	(1.04,3.28)
TRE	1.05	(0.50,1.59)	2.22	(0.63,3.81)
WSA	1.00	(0.61,1.38)	1.49	(0.91,1.95)
Male				
WPR	0.93	(0.72,1.15)	0.86	(0.68,1.04)
HPR	1.09	(0.36,1.81)	1.38	(0.72,2.03)
TRE	1.32	(0.52,2.11)	1.27	(0.77,1.76)
WSA	1.29	(0.84,1.73)	1.43	(1.08,1.78)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-1993 (19); female-1994 (6); male-1993 (9); male-1994 (5).
[c] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass.

Table 5.4. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for habitat inside 100% MCP for each hydrologic season for white-tailed deer in BCNP and ENP, November 1993 to April 1995.

	93DRY[b]		94WET		94DRY(FLOOD)	
Female						
WPR[c]	1.01	(0.81,1.20)	0.96	(0.77,1.16)	0.52	(0.25,0.79)
HPR	0.84	(0.32,1.36)	1.09	(0.49,1.69)	2.32	(1.21,3.44)
TRE	1.15	(0.37,1.93)	1.20	(0.52,1.88)	2.68	(0.28,5.08)
WSA	1.20	(0.46,1.94)	0.96	(0.60,1.32)	1.33	(0.82,1.84)
Male						
WPR	0.76	(0.44,1.09)	0.91	(0.63,1.18)	0.64	(0.28,1.00)
HPR	1.32	(0.21,2.43)	1.27	(0.31,2.23)	2.07	(0.63,3.51)
TRE	2.20	(0.44,3.96)	1.26	(0.32,2.20)	1.93	(1.06,2.80)
WSA	1.70	(0.90,2.50)	1.10	(0.56,1.64)	1.44	(0.60,2.27)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-93DRY (19); female-94WET (17); female-94DRY (8); male-93DRY (9); male-94WET (7); male-94DRY (5).
[c] WPR=wet prairie; HPR=herbaceous prairie; TRE=tree islands; WSA=willow/sawgrass.

Habitat selection was more pronounced when the selection ratios were based on radio-locations with habitat availability assumed equal for all individuals (Tables 5.5 and 5.6). In 1993, females exhibited selection for tree islands and willow/dense sawgrass and exhibited no selection for or against wet and herbaceous prairies. However, in 1994, females selected against wet prairie and for tree islands, exhibiting much stronger tendencies than in 1993. Using hydrologic seasons, a similar pattern was observed; in 94DRY(FLOOD), females strongly selected against wet prairie and for tree islands. For males, there was little change in the selection ratios from 1993 to 1994. In both years, males selected against wet prairie and for tree islands. Little change in the male habitat selection ratios was observed across the 3 hydrologic seasons.

Selection ratios, based on habitat availability within individual home ranges (100% MCP), reiterated the changes in habitat use as the flood progressed (Tables 5.7 and 5.8). Females selected against wet prairies and selected for tree islands more strongly in 1994 than in 1993. Additionally, females selected for willow/dense sawgrass areas in 1993, but exhibited no selection for or against willow/dense sawgrass in 1994, relative to the availability in their home ranges. Again, similar patterns were observed across hydrologic seasons, with an increasing selection for tree islands and increasing selection against wet prairie and willow/dense sawgrass as the flood waters deepened. For males, there was little change in the selection ratios on an annual basis or on a hydrologic season basis; they consistently selected against wet prairie and selected for tree islands, relative to the availability within their home ranges.

Table 5.5. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for radio-locations for each annual cycle for white-tailed deer in BCNP and ENP, September 1993 to August 1995.

	1993[b]		1994	
Female				
WPR[c]	0.83	(0.63,1.03)	0.32	(0.13,0.51)
HPR	0.81	(0.33,1.28)	1.50	(0.50,2.50)
TRE	2.41	(1.34,3.49)	6.49	(4.20,8.78)
WSA	2.08	(1.19,2.96)	1.53	(0.82,2.26)
Male				
WPR	0.29	(0.12,0.46)	0.23	(0.15,0.31)
HPR	1.11	(0.19,2.03)	1.45	(0.49,2.40)
TRE	6.77	(4.46,9.08)	6.56	(3.72,9.41)
WSA	2.81	(1.92,3.71)	2.83	(1.15,4.51)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-1993 (19); female-1994 (6); male-1993 (9); male-1994 (5).
[c] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass.

Table 5.6. Selection ratios and 95% Bonferroni confidence intervals[a] using the design II analysis for radio-locations for each hydrologic season for white-tailed deer in BCNP and ENP, November 1993 to April 1995.

	93DRY[b]		94WET		94DRY(FLOOD)	
Female						
WPR[c]	0.81	(0.62,1.00)	0.81	(0.60,1.00)	0.14	(0.05,0.23)
HPR	0.82	(0.34,1.30)	0.85	(0.44,1.26)	0.31	(0.66,1.97)
TRE	2.62	(1.43,3.81)	2.64	(1.60,3.68)	8.65	(6.97,10.32)
WSA	2.05	(1.04,3.06)	2.05	(0.92,3.18)	1.68	(0.73,2.63)
Male						
WPR	0.20	(0.06,0.35)	0.42	(0.13,0.71)	0.13	(0.04,0.23)
HPR	1.22	(0.15,2.28)	1.26	(0.54,1.71)	0.86	(0.28,1.45)
TRE	7.35	(4.81,9.89)	5.08	(2.46,7.71)	9.27	(6.90,11.64)
WSA	2.91	(1.81,4.00)	3.24	(1.78,4.70)	2.34	(0.09,4.59)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-93DRY (19); female-94WET (18); female-94DRY (10); male-93DRY (9); male-94WET (8); male-94DRY (6).
[c] WPR=wet prairie; HPR=herbaceous prairie; TRE=tree islands; WSA=willow/sawgrass.

Table 5.7. Selection ratios and 95% Bonferroni confidence intervals[a] using the design III analysis for each annual cycle for white-tailed deer in BCNP and ENP, September 1993 to August 1995.

	1993[b]		1994	
Female				
WPR[c]	0.82	(0.69,0.95)	0.53	(0.34,0.71)
HPR	0.89	(0.61,1.17)	0.71	(0.32,1.09)
TRE	2.29	(1.40,3.18)	2.95	(1.41,4.48)
WSA	2.08	(1.40,2.77)	1.07	(0.54,1.60)
Male				
WPR	0.31	(0.16,0.45)	0.27	(0.22,0.32)
HPR	1.06	(0.46,1.65)	1.06	(0.55,1.57)
TRE	5.10	(2.79,7.41)	5.17	(2.99,7.36)
WSA	2.19	(0.95,3.43)	1.98	(1.03,2.92)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-1993 (19); female-1994 (6); male-1993 (9); male-1994 (5).
[c] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass.

Table 5.8. Selection ratios and 95% Bonferroni confidence intervals[a] using the design III analysis for each hydrologic season for white-tailed deer in BCNP and ENP, November 1993 to April 1995.

	93DRY[b]		94WET		94DRY(FLOOD)	
Female						
WPR[c]	0.80	(0.70,0.91)	0.83	(0.68,0.99)	0.27	(0.15,0.38)
HPR	0.97	(0.70,1.25)	0.78	(0.49,1.06)	0.57	(0.24,0.91)
TRE	2.28	(1.27,3.29)	2.20	(1.26,3.14)	3.21	(0.72,5.71)
WSA	1.71	(1.02,2.40)	2.13	(1.06,3.21)	1.26	(0.33,2.19)
Male						
WPR	0.26	(0.12,0.40)	0.46	(0.23,0.69)	0.21	(0.12,0.29)
HPR	0.97	(0.47,1.48)	0.90	(0.50,1.29)	0.42	(0.16,0.68)
TRE	3.29	(1.21,5.36)	4.01	(2.50,5.51)	4.81	(3.05,6.57)
WSA	1.70	(0.53,2.86)	2.94	(0.86,5.01)	1.63	(0.42,2.83)

[a] Confidence intervals that do not include 1 indicate a selection against (selection ratio <1) or a selection for (selection ratio >1) a given habitat.
[b] Sample sizes: female-93DRY (19); female-94WET (17); female-94DRY (8); male-93DRY (9); male-94WET (7); male-94DRY (5).
[c] WPR=wet prairie; HPR=herbaceous prairie; TRE=tree islands; WSA=willow/sawgrass.

5.3. Discussion

The assumption that extended and extreme high water conditions negatively impacted the white-tailed deer population in the Everglades is substantiated by changes in survival rates, productivity rates, and spatial-use patterns.

The survival rates of females during the flood year (48%) were substantially lower than the mean annual rate (85%) during 1989-92 (Labisky et al. 1995, MacDonald 1997). Male survival rates also decreased during the flood year (54%) relative to the mean annual survival rate (67%) during 1989-92 (Labisky et al. 1995, MacDonald 1997). Of the adult male mortalities from 1989-92, 76% (16 of 21) occurred as a result of legal or illegal harvest, and none of the mortalities during the flood year were related to harvest as the hunting season had been cancelled. Thus, the flood did have severe consequences on the structure of this deer population. These high mortality rates were comparable to mortality rates experienced during previous floods in the Everglades (Loveless 1959b, Lampton 1982, Langenau et al. 1984).

Relative to productivity during 1989-92 and the year prior to the flood, productivity appeared to be depressed following the extended flood conditions of 1994-95 (MacDonald 1997). A decrease in productivity also was observed in 1993 following Hurricane Andrew (Labisky et al. 1999). This reduction in productivity may have been due to negative impacts of the environmental catastrophes (i.e., flood or hurricane) on the physical condition of the females brought on by stress and changes in diet or by an increase in predation of neonatal fawns.

Females demonstrated a substantial shift in habitat use during the flood by utilizing tree islands more heavily. This shift may have impacted feeding patterns, as the

preferred forage of the female is swamp lily, which is concentrated in the wet prairies. Males showed a small increase in use of tree islands from the preflood year to the flood year; however, these data also suggest that males were using tree islands more heavily in both years than during the normal to dry weather conditions of 1989-92 (calibration data). The similarity of habitat-use patterns of females and males during the flood represented a severe disruption in the sexually segregated social and spatial patterns of deer (Main et al. 1996).

Deer that survived the flood demonstrated high variability in degree of site fidelity; however, those that perished during the flood exhibited a low degree of site fidelity prior to death (MacDonald 1997). These deer that survived may have had the advantage of occupying an optimum location at a slightly higher elevation, thereby decreasing the necessity to leave in search of dry ground and forage. Thus, they probably were more fit to survive the extended flood conditions because they did not need to expend additional energy to find sufficient forage. Deer more familiar with their surroundings may be better able to elude predators. Those survivors that exhibited a lessor degree of site fidelity during the flood may have been better able to adapt to the change in environmental conditions and were successful in finding new home ranges, thus increasing the overall fitness of the population.

CHAPTER 6
VALIDATION OF THE SIMULATION MODEL UNDER FLOOD CONDITIONS

In this chapter, I discuss validation of the IBSE simulation model developed in Chapter 4 using both visual and statistical tools. I also discuss suggestions for the improvement of the model based on the validation results.

6.1. Approach to Model Validation

The white-tailed deer movement model was calibrated using radio-telemetry data collected on deer that were monitored from 1989 to 1992. To test the model's performance under alternative conditions, simulated deer movement patterns were evaluated under simulated flood conditions. These patterns were compared to the spatial- and habitat-use patterns of the white-tailed deer monitored during the flood of 1994-95 (Chapter 5).

Fifty runs of the simulation were conducted under flood conditions using the same set of algorithms and parameter values described for females and males in Section 4.4. Each run contained 30 deer started in random locations on the study site map (Fig. 4.9) using water depths at P-34 (centrally located water depth gauge), from 1992 to 1995.

Water depths used in the flood simulations were a combination of observed and artificial water levels (Fig. 6.1). As in the calibration simulations, each year corresponded to a biological year, which started on April 1. Since the first several years of the simulation had water depths that were the average monthly water depths between 1989

and 1992 [i.e., the same as those used for the calibration runs in Chapter 4 (see Table 4.2)], I assumed that burn-in time for these simulations was also 3 years. The 3 years used for simulation burn-in were YR1-B, YR2-B, and YR3-B (Fig 6.1). Data from the 4th and following years of the simulation were used in the validation analyses. The 4th year of the simulations (YR4) was used to establish steady-state values for the outcome measures prior to the stress of flood conditions, and were comparable to the 4th year of the calibration simulations since monthly water depths were the identical up to this point.

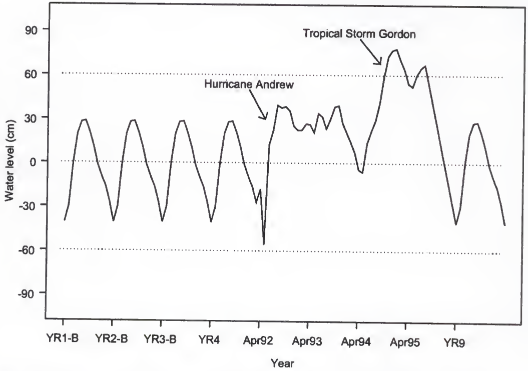

Figure 6.1. Monthly water depths at P-34 gauging station used for flood simulations. Depths for YR1-B, YR2-B, YR3-B, YR4, and YR9 were the mean monthly water depths from 1989-91 (same depths as used in model calibration), and years YR1-B, YR2-B, and YR3-B constituted the burn-in time for the simulation. From April 1992 to August 1995 (YR5 through the first half of YR8), observed mean monthly water depths were used. Flood conditions were artificially removed during the second half of YR8 by reducing water depths. YR9 monthly water depths were the same as those during YR1-B, YR2-B, YR3-B, and YR4.

From April 1992 to August 1995 (YR5 through the first half of YR8), actual mean monthly water depths at P-34 were used. Flood conditions were decreased artificially during the 7 months following August 1995 (the second half of YR8) by reducing water depths. The final year of the simulation (YR9) had water levels the same as those during the first 4 years of this simulation and the same as those in the calibration simulations.

Several analyses were performed to evaluate the simulation under flood conditions. First, plots of the outcome variables were used to examine trends over time. Second, predictive p-values were used to evaluate the likelihood that the values of the observed summary outcomes (e.g., female mean home range size from 93DRY obtained from the field data) could have arisen as an outcome of the simulation model for the hydrologic seasons of 93DRY, 94WET, and 94DRY(FLOOD). Finally, data from the 4th year of the simulation were compared to data from the 9th (final) year of the simulation, using mixed model analyses, to determine if the simulation had enough robustness for the summary outcomes to return to their preflood values.

In the following analyses, I focused on outcomes measured for each hydrologic season. Due to rapidly fluctuating water levels, changes in spatial- and habitat-use patterns were more readily observed with shorter time spans. Also, the annual cycles used for the calibration and validation data analyses were not directly comparable. Due to timing of commencement and completion of data collection, an annual cycle from April to March was used for the calibration data set, and an annual cycle from September to August was used for the validation data.

The outcomes evaluated for the model validation were home range size and percentage of observations in each of the four major habitats (wet prairie, herbaceous

prairie, tree islands, and willow/dense sawgrass). Because few deer in the validation data set were observed for a sufficient length of time to estimate distance between consecutive home range centers, this outcome measure was not evaluated in the validation analyses. Since mean distance between consecutive locations was determined to be a poor measure of goodness-of-fit (Section 4.6), it not used as an outcome measure.

6.2. Model Validation Results

6.2.1. Females

Variability in outcome measures among individuals was high (Fig. 6.2), similar to results observed under calibration water levels (Figs. 4.12, 4.13). During the 1st year after burn-in (the 1st year depicted in the plots), many females showed an increase in home range size from the wet to the dry hydrologic seasons. This finding was consistent with 1989-92 field data used for model calibration, in which females had larger home ranges during the dry season than the wet season. From 1992 to 1995, seasonal home range sizes decreased; however, by the end of the simulation run, home range sizes appeared to be increasing. Due to high variability among individual deer, visually discovering any clear temporal patterns was difficult. This difficulty was also present for percentage of observations in each of the four major habitats. Variation in habitat use was high both among individuals and among years.

Temporal patterns of mean summary outcomes from the 50 simulation runs were described through the use of plots (Fig. 6.3). Again, the increase in home range size from the wet season to the dry season during the 1st year after burn-in was evident. Seasonal shifts in home range size were not present between 92WET and 94WET, when home range sizes appeared slightly smaller than those observed during the wet season of the 1st

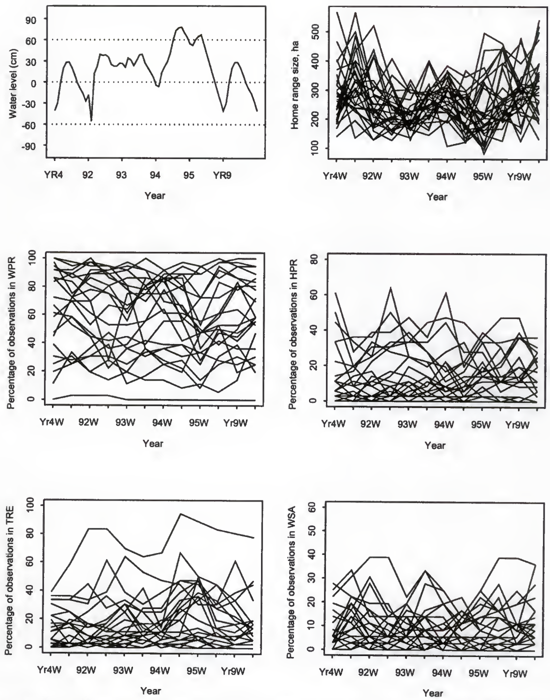

Figure 6.2. Monthly water depths and time trends for hydrologic-season home range size and percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) for 30 females from the 4th through 9th year of the validation runs. 'xxW' refers to the WET season of year 'xx'; unlabeled ticks refer to the corresponding DRY season. Each line represents one deer within a single simulation run.

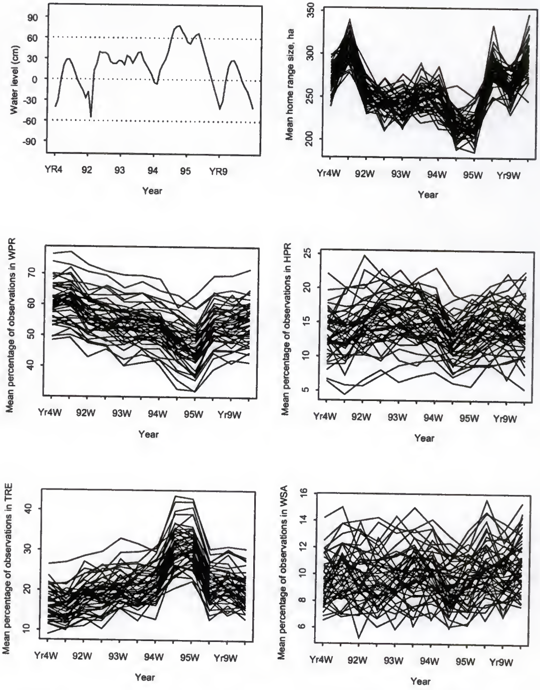

Figure 6.3. Monthly water depths and time trends for hydrologic-season home range size and percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) from the 4th through 9th year of the 50 validation runs (each with 30 females). 'xxW' refers to the WET season of year 'xx'; unlabeled ticks refer to the corresponding DRY season. Each line represents mean outcomes for one run.

year after burn-in. Home range size decreased again during 94DRY(FLOOD) and 95WET (the period of worst flooding). For the 3 postflood hydrologic seasons of the simulation, home range sizes appeared to return to the preflood sizes and seasonal patterns.

Temporal changes in habitat use also were more evident when simulation means were plotted (Fig. 6.3). Percentage of observations in the wet prairie decreased slightly during the 1st several years of the simulation, then decreased dramatically during 94DRY(FLOOD) and 95WET (the period of worst flooding) before returning to levels similar to those preflood. Mean percentage of observations in the herbaceous prairie appeared consistent over time except for a decrease in use during 94DRY(FLOOD). The temporal trend observed in the mean percentage of observations in tree islands was a mirror-image of the temporal trend observed in the mean percentage of observations in the wet prairie. Initially, mean percentage of observations in tree islands increased slightly each hydrologic season, a dramatic increase was observed during 94DRY(FLOOD) and 95WET, and was followed by a return to mean percentages similar to those observed preflood. No prominent temporal trend was visually discernable in the mean percentage of observations in willow/dense sawgrass.

Trends during 93DRY, 94WET, and 94DRY(FLOOD) were tested against the observed field data using predictive p-values (Tables 6.1, 6.2; Figs. 6.4, 6.5, 6.6). The predictive p-value analysis indicated a high likelihood that the values of the observed summary field data could have arisen as an outcome of the simulation model in 93DRY. In 94WET, mean home range sizes produced by the simulation were smaller than expected based on the field data; however, the average difference was only 50 ha (17% smaller). Despite the differences in home range size, habitat-use patterns (as measured by

mean percentage of observations in the four major habitats) were similar. In 94DRY(FLOOD), the period of most severe flooding for which field data were available, simulated deer constricted their home ranges and shifted habitat use from wet prairie to tree islands (Table 6.1), but not as much as expected, based on the observed data (Table 5.2).

To evaluate the ability of the simulated deer to return to an "initial state" following the stress of flood conditions, summary outcomes from hydrologic seasons in the 4th year (1st year following burn-in) and the 9th year (same water levels as in the 4th year) were compared (Table 6.3). For each of the summary measures, there was a significant difference ($p<0.01$) between the outcomes for the 4th year and the 9th year, indicating that the simulation had not returned to its initial state. However, most of the differences between the 4th and 9th years were biologically insignificant. Between the 4th simulation year and the 9th simulation year, the mean decrease in home range size was 9 ha (3% decrease from the 4th simulation year), and mean changes in percentage of observations in herbaceous prairie and willow/dense sawgrass were <1 percentage point (7% and 8% increase, respectively). However for mean percentage of observations in wet prairie and in tree islands, the differences were larger. Observations in the wet prairie decreased, on average, by 7 percentage points (12% decrease), and observations in the tree islands increased, on average, by 5 percentage points (31% increase). Habitat use returned to a distribution similar to that observed in the simulation during 93DRY and 94WET, the 2 hydrologic seasons immediately preceding the flood (Table 6.1).

Table 6.1. Mean outcome measures from the 93DRY, 94WET, and 94DRY(FLOOD) hydrologic seasons of 50 simulation runs (each with 30 females).

Outcome measure	93DRY		94WET		94DRY	
Home range size, ha	252	(2)	249	(2)	217	(2)
Percentage of observations in each habitat						
Wet prairie	53	(0.8)	53	(0.8)	48	(0.9)
Herbaceous prairie	15	(0.5)	15	(0.4)	12	(0.4)
Tree islands	21	(0.6)	22	(0.6)	31	(0.7)
Willow/dense sawgrass	10	(0.3)	10	(0.2)	9	(0.2)

[a] Standard error in parentheses.

Table 6.2. Predictive p-values from the 93DRY, 94WET, and 94DRY(FLOOD) hydrologic seasons of 50 simulation runs (each with 30 females).

Outcome measure	93DRY	94WET	94DRY
Home range size, ha	0.12	0.00	0.00
Percentage of observations in each habitat			
Wet prairie	0.18	0.12	0.00
Herbaceous prairie	0.30	0.28	0.02
Tree islands	0.32	0.10	0.00
Willow/dense sawgrass	0.38	0.48	0.46

Table 6.3. Mean hydrologic season outcome measures from the 1st year after burn-in (year 4) and the last year (year 9) of 50 simulation runs (each with 30 females).

Outcome measure	Yr 4 WET		Yr 4 DRY		Yr 9 WET		Yr 9 DRY	
Home range size, ha	271	(2)	307	(2)	264	(2)	297	(3)
Percentage of observations in each habitat								
Wet prairie	61	(0.8)	61	(0.9)	54	(0.8)	55	(0.8)
Herbaceous prairie	13	(0.4)	13	(0.5)	15	(0.5)	14	(0.5)
Tree islands	17	(0.5)	16	(0.5)	22	(0.6)	20	(0.6)
Willow/dense sawgrass	9	(0.2)	10	(0.3)	10	(0.2)	11	(0.3)

[a] Standard error in parentheses.

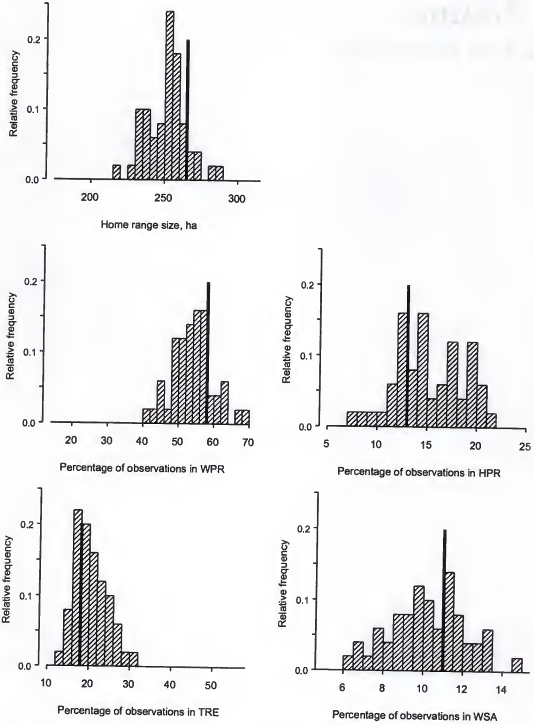

Figure 6.4. Distributions of mean summary outcomes during 93DRY from 50 simulation runs (each with 30 females). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

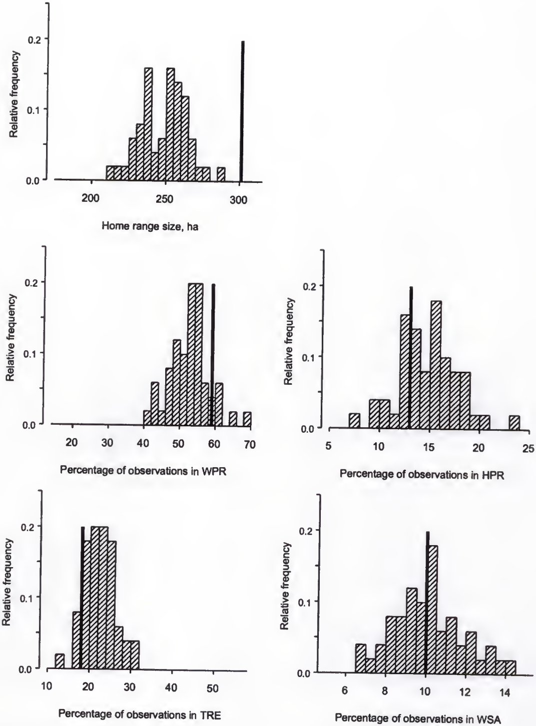

Figure 6.5. Distributions of mean summary outcomes during 94WET from 50 simulation runs (each with 30 females). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

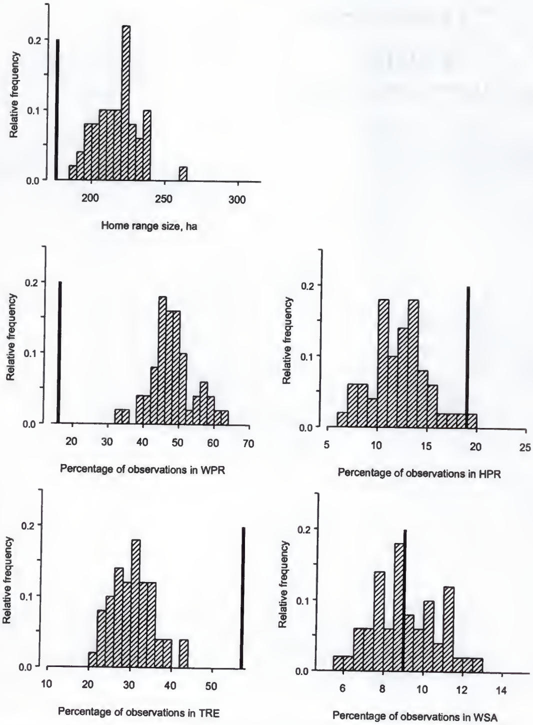

Figure 6.6. Distributions of mean summary outcomes during 94DRY(FLOOD) from 50 simulation runs (each with 30 females). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

6.6.2. Males

Variability in outcome measures among individuals was high (Fig. 6.7), similar to results observed under calibration water levels (Figs. 4.20, 4.21). Most simulated males had smaller home ranges during the dry season than during the wet season, consistent with patterns observed from 1989-92. Variation in home range sizes appeared to be greater during periods when deer experienced water deeper than in the calibration simulations during rut (i.e., 93WET, 94WET, and 95WET). No temporal trends were visually discernable for the percentage of observations in wet prairie, herbaceous prairie, or willow/dense sawgrass; however, the percentage of observations in tree islands appeared to increase over the span of the simulation run. Variation in habitat use was high among individuals and years.

Temporal patterns of the mean summary outcomes from the 50 simulation runs were described through the use of plots (Fig. 6.8). As with female simulations, plots of mean summary outcomes were more informative with regard to overall trends than plots of individual summary outcomes. Mean home range size was consistently larger during the wet seasons than it was during the dry seasons; however, no changes were evident as a result of flooding. As with the flood simulations for females, mean percentage of observations in wet prairie was a mirror-image of mean percentage of observations in tree islands. For the first several years of the simulation (through 94WET), percentage of observations in wet prairie decreased gradually and percentage of observations in tree islands increased slowly. In 94DRY(FLOOD), use of wet prairie dropped dramatically and use of tree islands increased dramatically. Following 94DRY(FLOOD), percentage of observations in wet prairie and in tree islands returned to pre-flood levels. Percentage of

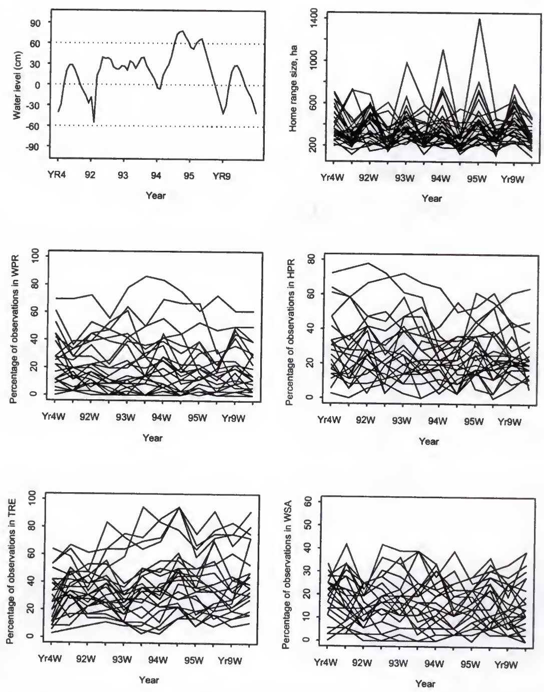

Figure 6.7. Monthly water depths and time trends for hydrologic-season home range size and percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) for 30 males from the 4[th] through 9[th] year of the validation simulations. 'xxW' refers to the WET season of year 'xx'; unlabeled ticks refer to the corresponding DRY season. Each line represents one deer within a single run.

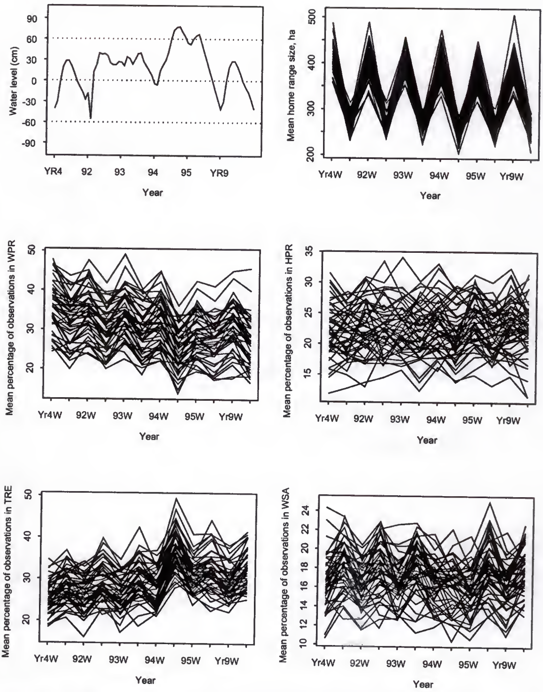

Figure 6.8. Monthly water depths and time trends for hydrologic-season home range size and percentage of observations in wet prairie (WPR), herbaceous prairie (HPR), tree islands (TRE), and willow/dense sawgrass (WSA) from the 4th through 9th year of the 50 validation runs (each with 30 males). 'xxW' refers to the WET season of year 'xx'; unlabeled ticks refer to the corresponding DRY season. Each line represents mean outcomes for one run.

observations in herbaceous prairie and willow/dense sawgrass exhibited no discernable temporal trends, except for a possible decrease in the percentage of observations in willow/dense sawgrass during the periods of deepest water.

Summary outcomes during 93DRY, 94WET, and 94DRY(FLOOD) were tested against the observed field data using predictive p-values (Tables 6.4, 6.5; Figs. 6.9, 6.10, 6.11). The simulation consistently produced mean home range sizes that were larger than those observed in the field during 93DRY, 94WET, and 94DRY(FLOOD). The simulation performed better, although not perfectly, with respect to mean percentage of observations in the four major habitats. In 93DRY, it was unlikely that values of the

Table 6.4. Mean outcome measures from the 93DRY, 94WET, and 94DRY(FLOOD) hydrologic seasons of 50 simulation runs (each with 30 males).

Outcome measure	93DRY		94WET		94DRY	
Home range size, ha	265	(3)	397	(4)	251	(2)
Percentage of observations in each habitat						
Wet prairie	30	(0.8)	32	(0.8)	25	(0.7)
Herbaceous prairie	22	(0.6)	23	(0.6)	22	(0.6)
Tree islands	30	(0.6)	28	(0.6)	37	(0.7)
Willow/dense sawgrass	18	(0.4)	17	(0.3)	16	(0.3)

[a] Standard error in parentheses.

Table 6.5. Predictive p-values from the 93DRY, 94WET, and 94DRY(FLOOD) hydrologic seasons of 50 simulation runs (each with 30 males).

Outcome measure	93DRY	94WET	94DRY
Home range size, ha	0.00	0.00	0.00
Percentage of observations in each habitat			
Wet prairie	0.00	0.32	0.00
Herbaceous prairie	0.34	0.12	0.40
Tree islands	0.00	0.00	0.00
Willow/dense sawgrass	0.10	0.40	0.02

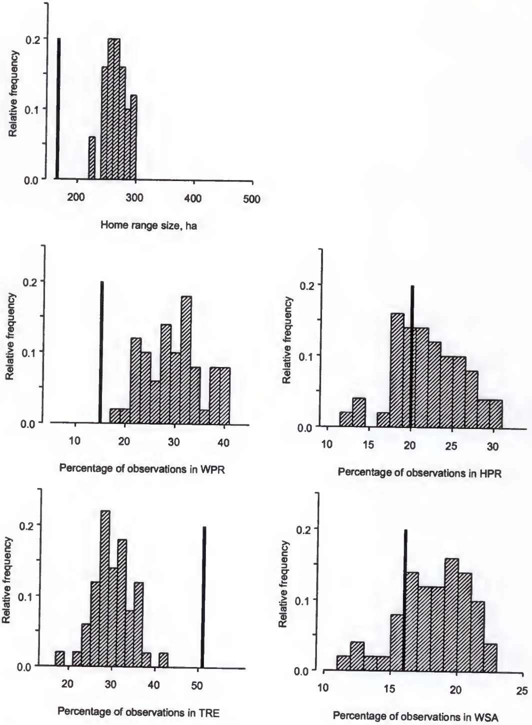

Figure 6.9. Distributions of mean summary outcomes during 93DRY from 50 simulation runs (each with 30 males). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

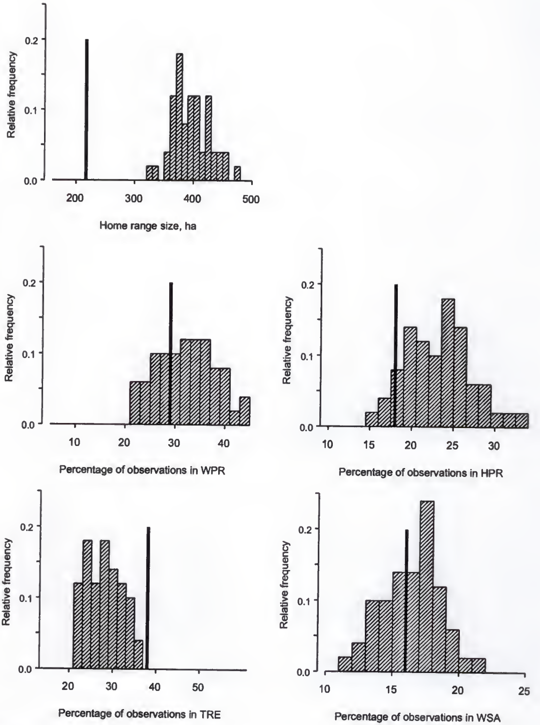

Figure 6.10. Distributions of mean summary outcomes during 94WET from 50 simulation runs (each with 30 males). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

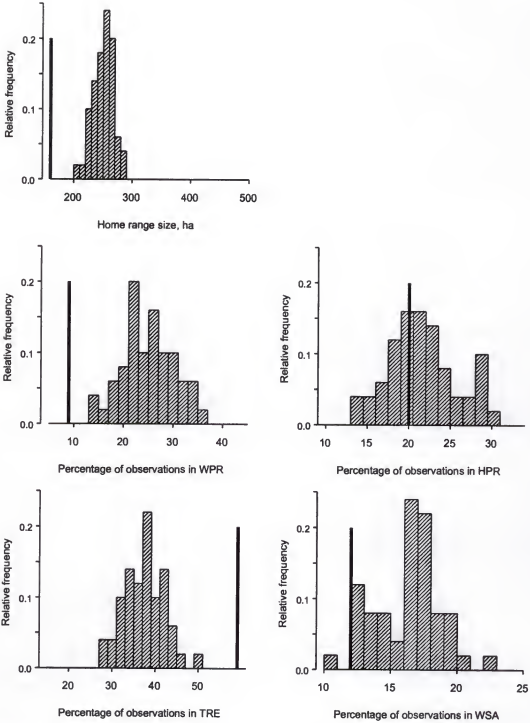

Figure 6.11. Distributions of mean summary outcomes during 94DRY(FLOOD) from 50 simulation runs (each with 30 males). Heavy vertical line represents the mean annual summary outcome from the field data. Note: WPR = wet prairie, HPR = herbaceous prairie, TRE = tree island, WSA = willow/dense sawgrass.

observed summary outcomes would have arisen as an outcome of the simulation, as the simulation produced summary outcomes that overpredicted the percentage of observations in wet prairie and underpredicted the percentage of observations in tree islands. In 94WET, the simulation model provided better predictions for habitat use than in 93DRY. The percentage of observations in tree islands was still less than expected based on the observed data, but the discrepancy was not as great as in 93DRY. In 94DRY(FLOOD), as in 93DRY, the simulation produced summary outcomes that overpredicted the percentage of observations in wet prairie and underpredicted the percentage of observations in tree islands. The simulation was sensitive to flood conditions, as the percentage of observations in wet prairie decreased and percentage of observations in tree islands increased during 94DRY(FLOOD), relative to 93DRY and 94WET (Table 6.4); however these changes were less than those observed in the field (Table 5.2).

To evaluate the ability of the simulated male deer to return to an initial state following the stress of the flood conditions, summary outcomes from the hydrologic seasons in the 4th year (1st year following burn-in) and the 9th year (same water levels as in the 4th year) were compared (Table 6.6). For percentage of observations in willow/dense sawgrass, there was no significant difference ($p=0.2439$) between the outcomes for the 4th year and the 9th year. For the rest of the summary measures, there was a significant difference ($p<0.05$) between the outcomes for the 4th year and the 9th year, indicating that the simulation model had not returned its initial state. However, several of the differences between the 4th and 9th years were small, even though they were statistically significant. Between the 4th simulation year and the 9th simulation year, the mean change in home

range size was 10 ha (3% decrease), and mean change in percentage of observations in herbaceous prairie was <1 percentage point (4% increase). For mean percentage of observations in wet prairie and in tree islands, the differences were larger. Observations in the wet prairie decreased, on average, by 5 percentage points (15% decrease), and observations in the tree islands increased, on average by 4 percentage points (19% increase). Habitat use approached a distribution similar to that observed in the simulation during 93DRY and 94WET, the 2 hydrologic seasons immediately preceding the flood (Table 6.1).

Table 6.6. Mean hydrologic season outcome measures from the 1st year after burn-in (year 4) and the last year (year 9) of 50 simulation runs (each with 30 males).

Outcome measure	Yr 4 WET		Yr 4 DRY		Yr 9 WET		Yr 9 DRY	
Home range size, ha	412	(4)	267	(3)	397	(5)	259	(3)
Percentage of observations in each habitat								
Wet prairie	36	(0.9)	32	(0.9)	31	(0.8)	27	(0.8)
Herbaceous prairie	22	(0.6)	22	(0.5)	23	(0.6)	23	(0.6)
Tree islands	25	(0.5)	28	(0.5)	29	(0.5)	33	(0.6)
Willow/dense sawgrass	17	(0.4)	18	(0.4)	16	(0.3)	18	(0.3)

[a] Standard error in parentheses.

6.3. Discussion

Validation with radio-telemetry data obtained during the flood of 1994-95 indicated that the proposed simulation model was sensitive to flood conditions, but also revealed the movement patterns of the simulated deer did not shift as much as expected. There are several potential reasons that may explain the lack-of-fit of the simulation model to the observed field data.

6.3.1. Quantity and Quality of Validation Field Data

First, the number of deer included in the validation data set (23 females and 13 males) was smaller than the number of deer included in the calibration data set (27 females and 19 males), and many of the deer in the validation data set were monitored for a shorter time period. Therefore, the validation data may not have been representative of the whole time interval [93DRY, 94WET, and 94DRY(FLOOD)]. For example, in the validation data set, only two males were monitored during all 3 hydrologic seasons, and four of the six males monitored during 94DRY(FLOOD) were not monitored during any other time intervals.

Simulated deer started the simulation by being randomly placed throughout the study area; however, the deer included in the validation data may not have been representative of the entire study area (Figs. 6.12, 6.13). Because the boundary between BCNP and ENP roughly divides the study area in half, management area residence provided an indication of the spatial distribution the radio-monitored deer. For the calibration data, 52% (15 of 29) of the females resided in BCNP with the remainder residing in ENP, and 24% (4 of 17) of the males resided in BCNP with 6% (1 of 17) residing in both management areas and the remainder residing in ENP. For the validation data, the females were reasonably divided with 48% (11 of 23) residing in BCNP, 22% (5 of 23) residing in both management areas, and 30% (7 of 23) residing in ENP. However, no males in the validation data set were residents of BCNP whereas 23% (3 of 13) were residents of both management areas and 77% (10 of 13) were residents of ENP.

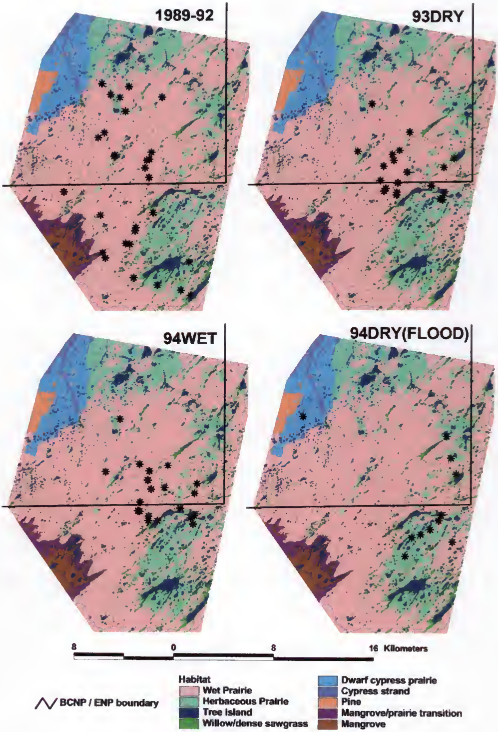

Figure 6.12. Home range centers of females included in the calibration data set (1989-92) and the 3 hydrologic seasons of the validation data set [93DRY, 94WET, 94DRY(FLOOD)].

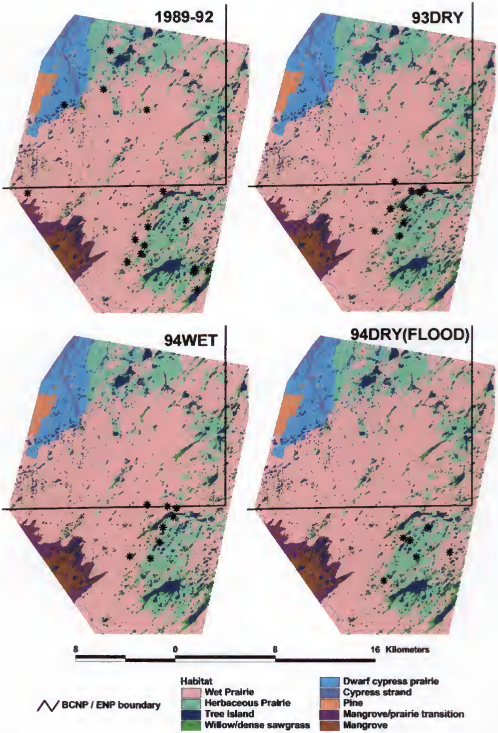

Figure 6.13. Home range centers of males included in the calibration data set (1989-92) and the 3 hydrologic seasons of the validation data set [93DRY, 94WET, 94DRY(FLOOD)].

Several potentially serious implications of the imbalance in the temporal and spatial distributions of the validation data set exist. In the simulation runs, all deer were present for all time intervals, but in the validation data, entry and exit from the data set was staggered. The staggered entries were due to deer being captured and entered into the study at a later date, whereas the staggered exits were due to failed radio-transmitters, death, or relocation outside the study area. In addition, the simulated data and the validation data may not have represented the same population of deer in a spatial framework. Males in the validation data set were heavily biased towards residence in ENP whereas simulated males had random starting locations in either management area. Thus, comparisons between the simulated flood data and validation data indicated lack-of-fit, but perhaps not because the model did an inadequate job of simulating deer movement. The lack-of-fit may have been because deer in the simulation were monitored for the entire time period and were located throughout the study area whereas many deer (especially males) in the validation data set represented fewer than 3 hydrologic seasons and only a small portion of the study area.

6.3.2. Factors Not Included in the Simulation Model

Habitat and water maps with more detail may have improved the predictive abilities of the simulation model. Although the habitat map had an accuracy of 80%, the habitat classifications were very broad. Within these broad classifications used by Miller (1993), a great deal of heterogeneity existed within each habitat. For example, no distinction was made between hardwood hammocks, which are rarely inundated, and bayheads, which are more frequently inundated. Although wet prairies are the most species-rich of the Florida marshes (Kushlan 1990), in this application, they were

considered homogenous both in elevation and in appeal relative to other habitats. An example of the complexity of the prairie/tree island/slough landscape was provided by Hunter's (1990) map of a 112 km^2 study area in the Taylor Slough (south central Everglades, see Fig. 2.1) which contained >100 habitat classifications.

The hydrology of the Everglades is not as simple as is portrayed by the temporal water-depth map used for these simulations. Although the centrally located water gauge (P-34) provided an indication of water depth over the study area, local topography and the status of proximate anthropogenic canals and pumps also influenced water depth. A more detailed simulation model of Everglades hydrology under natural and current water management schemes was developed by Fennema et al. (1994); however, the scale was too large to be suitable for the deer movement model presented in this study.

In addition, inclusion of mortality, as a function of the environment, may have improved the predictive capacities of the simulation model. Deer stranded in deep water during the Everglades flood of 1994-95 were more likely to either die or emigrate than those with access to higher ground and sufficient browse (MacDonald 1997). However, those deer that chose to emigrate faced additional stresses due to traveling. These movements likely increased their mortality rates. In the simulation, deer had the possibility of emigrating to areas of higher ground, but there was a distinct chance that they would never locate high ground. These stranded simulated deer may have spent ≥3 months in 60 cm of water with no ill effects because mortality was not included in the model. Some simulated individuals successfully sought and found tree islands during the flood, whereas others maintained a consistently high percentage of observations in the wet prairie and a negligible percentage (i.e., <5%) of observations in tree islands (see

Figs. 6.2 and 6.6 for examples). These stranded deer may have impacted the summary outcomes for the simulations by increasing the mean percentage of observations in the prairie and reducing the mean percentage of observations in the tree islands. If deer that were unsuccessful in finding refuge and forage on higher ground had a high probability of dying (i.e., being removed from the simulation during the flood), then the summary outcome measures for the 'surviving' deer may better represent observations from the field.

To augment the addition of mortality as a function of environment, the inclusion of additional population dynamics into the simulation model may have improved its predictive abilities. In the current model, the deer population remained static with 30 individuals (all either female or male) with no interactions among them. Increasing the number of deer to observed density levels and including deer-to-deer interactions may further improve the credibility of the simulation. Formation of matriarchal groups in females and territory defense in males could be added. Mortality, as a function of predation, age, and other causes, as well as fecundity could be included in the simulation.

6.3.3. Issues Involving Movement Algorithms Used in the Model

Although including population dynamics in the simulation may improve the performance of the model relative to the validation data, issues involving the current algorithms also should be addressed. Efforts should be made to further minimize burn-in time. If the number of deer in the simulation was increased to approximate typical population densities and interactions among deer were included, the CPU time to complete one run of the simulation would drastically increase. As simulation time increases, the proportion of computer time allotted to simulation burn-in becomes more

relevant. A goal of achieving consistent simulation burn-in within 1 or 2 years of simulation is realistic, and the best approach is most likely through further experimentation with the homing beacon and pixel memory algorithms. The issue of burn-in time also becomes more complicated when fecundity is added to the simulation. As each new deer is 'added' to the population, it will need time to explore its surroundings and create a home range. This additional level of complexity provides further motivation to reduce burn-in time.

Home range size of males also should be addressed, as the simulation tended to yield home ranges larger than expected. Smaller home ranges were obtained with minimal alteration of simulation parameters, but the trade-off was an increase in burn-in time. Again, further experimentation with the homing beacon and pixel memory algorithms, and possibly the introduction of additional algorithms, may produce home range size estimates closer to the observed field data. Further analyses could be done using the existing field data and simulation data to determine if using the kernel density estimator for home range size was appropriate or if a different home range estimator (e.g., minimum convex polygon) would be more descriptive, given the spatial distributions of the observed and simulated radio-locations.

A final area of exploration is to further investigate why the simulation outcomes did not return to their 'initial' steady-state after flood conditions were relaxed in the validation simulations. Although the simulated outcomes moved towards their initial state during the year following the flood, they did not return to that initial state. One hypothesis was that the water conditions that existed in the simulation between 92WET and 93WET (after burn-in, but before the flood) moved the model processes to a new, different

equilibrium. With longer simulation runs and runs using different hypothetical temporal water-depth patterns, the temporal dynamics of these movement processes could be examined further.

CHAPTER 7
CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

The objective of this study was to develop an IBSE simulation model of movement patterns of adult white-tailed deer in the Florida Everglades. The model provided a means of exploring patterns of spatial use of deer in response to environmental catastrophes (e.g., tropical storms) and to different management regimes (e.g., water control). While conducting the initial phase of model development, I was unable to locate guidelines or a framework for the calibration of an IBSE simulation model. Therefore, a major focus of this research became the development and documentation of such a process. Although none of the tools used in the calibration process were new, formalizing their use in an organized iterative fashion for model development and calibration (Fig. 4.4) was a pioneering exercise.

The specific objective of the simulation model was to predict how temporal landscape changes (i.e., rising and falling water levels) would affect movement patterns of deer in the Florida Everglades. This objective required calibration and validation procedures. Calibration issues focused on discrepancy measures to test IBSE model output relative to observed data, an iterative approach for calibrating an IBSE model with sequential experimentation, and evaluation of the predictive abilities of an IBSE simulation using predictive p-values. The algorithms and parameterization of the initial model were presented and two of the sequential calibration experiments for females were

discussed in detail. The final model for females and males was presented and the final evaluation, using predictive p-values, was discussed. After the model was sufficiently calibrated, validation was performed using radio-telemetry data collected just prior to and during the flood of 1994-95. Based on the results of the validation analyses, several suggestions for improvement of the movement model were considered.

7.1. Applications of the White-tailed Deer Movement Simulation Model

This movement model, after concerns revealed during validation were addressed, can be used to predict the status of white-tailed deer in the unstable ecosystem of the Everglades. Additional validation could be conducted by assessment of performance of the simulation relative to radio-telemetry data collected from white-tailed deer in other areas of the Everglades. For example, the model could be run using habitat maps from the Taylor Slough area and evaluated with the data collected by Hunter (1990).

One use of this model is as one of the many tools for planning Everglades restoration (Fleming et al. 1994, USGS 1997, DeAngelis et al. 1998). The working hypothesis for the restoration program is that a return to natural hydrological conditions will result in a substantial recovery of many characteristic and endangered species in the region. Part of this large restoration effort has been the development of the suite of simulation models, Across Trophic Level System Simulation (ATLSS), to predict and compare the effects of alternative hydrologic scenarios on this ecosystem. The movement algorithms for deer that I developed could be incorporated into the model as a comparison to the deer component currently used in the ATLSS model.

Another potential application of the model would be to predict the impact of catastrophic events on white-tailed deer in south Florida. On average, south Florida is

subjected to a tropical storm once every 3 years. Some of those storms are relatively dry, like Hurricane Andrew in 1992, and some are extremely wet, like Tropical Storm Gordon in 1994. Although both storms had a devastating impact on the human population and human-built structures, each storm had a different impact on the deer population. This simulation model can aid in predicting the level and longevity of the impact on the deer population, for various scenarios such as strong hurricanes several years in a row, or several hurricanes in a single year.

7.2. Contributions to the Field of Ecological Modeling

The set of calibration tools and the iterative approach developed and demonstrated in this dissertation provides a framework for more rigorous evaluation of simulation models. Although the techniques were presented in the context of IBSE simulation models, they could be applied to the development, calibration, and validation of other classes of simulation models as well.

Burn-in time was explored as a nuisance parameter of simulations, and a technique for its estimation is presented. During my literature review, I found only one IBSE simulation model in which the issue of burn-in was addressed. Risenhoover et al. (1997) allowed deer in their simulation to move and interact with the landscape for 1 year to provide a realistic dispersion of animals. However, they gave no justification for the length of the initialization time.

Simulation model building was presented as an iterative process in which the developer constantly reevaluates the model and updates algorithms and parameter values to obtain the best fit possible. This systematic, iterative approach aids in the search for the optimum model algorithms and parameter settings that best represent the system of

interest. Discrepancy measures, experimental design, and analysis techniques were presented as tools for the calibration of IBSE simulation models.

Based on the calibration and validation results for the model presented in this dissertation, several cautions should be made regarding predictive abilities and accuracy of any simulation model. As Box (1982: 117) noted, "all models are wrong; some models are useful." The difficulty then lies in determining which models are useful. Thus, adequate model validation is necessary for predictive accuracy. For example, in the model developed in this dissertation, final evaluation indicated that the model performed well using the water conditions under which it was developed. Although the simulated deer were sensitive to flood conditions, the sensitivity was not as high as expected when compared to the validation data that was collected during the flood. With the guidelines and detailed descriptions of the model development, verification, calibration, and validation of the model presented in this dissertation, the tools for building defensible models are now more approachable.

APPENDIX A
CALIBRATION DATA SET

Table A.1. Age, residence, and number of radio-locations for radio-collared white-tailed deer included in calibration data set.

Deer ID	Capture Date	Age[a]	Residence	Number of observations[b] 1989	1990	1991	Status as of 31 March 1992
Female							
89002	29 Mar 89	4	BCNP	58	77	67	Alive
89004	05 Apr 89	4	BCNP	59	73	-[c]	Dead: alligator predation, 02 Sep 91
89005	05 Apr 89	1	BCNP	59	73	-	Censored, 08 Feb 92
89008	05 Apr 89	2	BCNP	59	76	66	Alive
89014	06 Apr 89	3	BCNP	56	75	-	Alive, radio-collar failed 07 Sep 91
89016	06 Apr 89	1	ENP	55	-	-	Dead: bobcat predation, 20 May 90
89019	10 May 89	4	ENP	51	-	-	Dead: bobcat predation, 16 Mar 90
89021	10 May 89	3	ENP	53	75	-	Censored, 24 Sep 91
89022	10 May 89	3	ENP	56	74	-	Censored, 04 Dec 91
89026	10 May 89	2	ENP	56	76	-	Dead: undetermined cause, 02 Mar 91
89041	28 Jun 89	6	BCNP	-	78	66	Alive
89045	28 Jun 89	4	ENP	-	74	67	Alive
89055	14 Aug 89	3	BCNP	-	76	70	Alive
89058	14 Aug 89	4	BCNP	-	75	69	Alive
89059	14 Aug 89	3	BCNP	-	59	-	Dead: bobcat predation, 12 Jan 91
89062	14 Aug 89	2	ENP	-	77	-	Censored, 21 Dec 91
89063	14 Aug 89	3	ENP	-	84	69	Alive
90067	06 Jan 90	4	BCNP	-	81	79	Alive
90069	06 Jan 90	4	BCNP	-	72	-	Alive, radio-collar failed 20 May 91

Table A.1. – continued.

Deer ID	Capture Date	Age	Residence	Number of observations			Status as of 31 March 1992
				1989	1990	1991	
Female							
90081	09 Mar 90	4	BCNP	-	75	61	Censored, 25 Jan 92
90107[d]	12 Apr 90	1	BCNP	-	-	68	Alive
90123	03 Aug 90	3	ENP	-	-	67	Alive
90124	03 Aug 90	3	ENP	-	-	67	Alive
90125	03 Aug 90	3	ENP	-	-	63	Alive
90129	15 Aug 90	4	ENP	-	-	67	Alive
90131	15 Aug 90	3	BCNP	-	-	68	Alive
90135	16 Aug 90	3	BCNP	-	-	67	Alive
90138	16 Aug 90	4	ENP	-	-	70	Alive
90141	17 Aug 90	6	ENP	-	-	63	Alive
Male							
89003[e]	05 Apr 89	1	BCNP	-	76	-	Alive, dispersed from study area in Oct 91
89017	06 Apr 89	1	BCNP	58	-	-	Dead: legal kill, 26 Nov 90
89023	10 May 89	1	ENP	52	-	-	Censored, 04 Aug 90
89025	10 May 89	4	ENP	52	75	-	Censored, 28 May 91
89027	10 May 89	3	BCNP/ENP	54	-	-	Dead: illegal kill, 15 Sep 90
89033	11 May 89	4	ENP	55	74	64	Alive
89034	11 May 89	5	ENP	54	80	64	Alive
89046	28 Jun 89	4	ENP	-	77	68	Alive

Table A.1. – continued.

Deer ID	Capture Date	Age	Residence	Number of observations			Status as of 31 March 1992
				1989	1990	1991	
Male							
89052	29 Jun 89	3	ENP	-	78	68	Alive
89060	14 Aug 89	4	ENP	-	75	68	Alive
89061	14 Aug 89	4	ENP	-	77	-	Dead: undetermined cause, 28 Nov 91
90078	09 Mar 90	1	BCNP	-	80	-	Dead: legal kill, 16 Nov 91
90091	21 Mar 90	5	ENP	-	77	68	Alive
90109	13 Apr 90	4	ENP	-	73	-	Dead: illegal kill, 11 Nov 91
90119	28 Jun 90	4	BCNP	-	-	67	Alive
90128	15 Aug 90	4	ENP	-	-	67	Alive
90130	15 Aug 90	4	ENP	-	-	64	Alive

[a] Age (years) as of date entered into the calibration data set.
[b] Annual cycles are: 1989 (01 Apr 89 - 31 Mar 90), 1990 (01 Apr 90 - 31 Mar 91), and 1991 (01 Apr 91 - 31 Mar 92).
[c] Either deer not monitored or <50 radio-locations during annual cycle.
[d] Captured as a fawn, not included in calibration data set until 1 April 1991.
[e] Captured as a fawn, not included in calibration data set until 1 April 1990.

Table A.2. Annual home range statistics for 46 radio-collared white-tailed deer included in calibration data set.

Deer ID	Home range size (ha)			Distance between centers (m)[a]		Mean distance between consecutive locations (m)		
	1989	1990	1991	1989-90	1990-91	1989	1990	1991
Female								
89002	395	317	406	215	287	746	756	668
89004	400	228	-	159	-	1186	569	-
89005	236	160	-	417	-	934	560	-
89008	386	280	270	294	305	955	706	722
89014	303	188	-	209	-	747	581	-
89016	202	-	-	-	-	849	-	-
89019	280	-	-	-	-	706	-	-
89021	141	90	-	291	-	448	415	-
89022	209	337	-	122	-	571	852	-
89026	101	97	-	55	-	322	339	-
89041	-	185	302	-	625	-	537	770
89045	-	441	323	-	239	-	902	810
89055	-	239	173	-	465	-	601	615
89058	-	148	201	-	138	-	465	645
89059	-	281	-	-	-	-	774	-
89062	-	123	-	-	-	-	395	-
89063	-	145	188	-	748	-	472	510
90067	-	359	332	-	39	-	705	779
90069	-	600	-	-	-	-	1014	-

Table A.2. – continued.

Deer ID	Home range size (ha)			Distance between centers (m)		Distance between consecutive locations (m)		
	1989	1990	1991	1989-90	1990-91	1989	1990	1991
Female								
90081	-	562	403	-	614	-	765	1138
90107	-	-	171	-	-	-	-	545
90123	-	-	249	-	-	-	-	686
90124	-	-	220	-	-	-	-	604
90125	-	-	289	-	-	-	-	628
90129	-	-	276	-	-	-	-	789
90131	-	-	219	-	-	-	-	629
90135	-	-	359	-	-	-	-	875
90138	-	-	302	-	-	-	-	573
90141	-	-	405	-	-	-	-	786
Male								
89003	-	334	-	-	-	-	715	-
89017	552	-	-	-	-	1696	-	-
89023	270	-	-	-	-	576	-	-
89025	177	219	-	226	-	553	782	-
89027	640	-	-	-	-	1306	-	-
89033	179	166	224	106	148	484	533	654
89034	140	137	102	54	299	383	315	375
89046	-	340	341	-	237	-	777	863

Table A.2. -- continued.

Deer ID	Home range size (ha)			Distance between centers (m)		Distance between consecutive locations (m)		
	1989	1990	1991	1989-90	1990-91	1989	1990	1991
Male								
89052	-	286	269	-	189	-	795	957
89060	-	344	377	-	592	-	911	1174
89061	-	149	-	-	-	-	432	-
90078	-	396	-	-	-	-	1209	-
90091	-	322	294	-	333	-	752	720
90109	-	268	-	-	-	-	684	-
90119	-	-	1086	-	-	-	-	1234
90128	-	-	352	-	-	-	-	822
90130	-	-	253	-	-	-	-	558

[a] Distance between consecutive annual home range centers.

Table A.3. Annual habitat use (percentage of observations in each habitat) for white-tailed deer included in calibration data set.

Deer ID	Year[a]	WPR[b]	HPR	TRE	WSA
Female					
89004	1990	58.9	11.0	17.8	12.3
89005	1990	46.6	5.5	26.0	21.9
89008	1991	56.1	15.2	12.1	16.7
89014	1990	37.3	24.0	18.7	20.0
89016	1989	69.1	1.8	12.7	16.4
89022	1989	57.1	0.0	28.6	14.3
89026	1989	19.6	46.4	26.8	7.1
89041	1990	23.1	43.6	30.8	2.6
89045	1991	58.2	16.4	20.9	4.5
89055	1990	31.6	46.1	19.7	2.6
89058	1990	25.3	32.0	32.0	10.7
89059	1990	88.1	1.7	3.4	6.8
89062	1990	5.2	67.5	18.2	9.1
89063	1990	29.8	2.4	58.3	9.5
90067	1991	75.9	8.9	6.3	8.9
90069	1990	79.2	8.3	5.6	6.9
90081	1991	80.3	4.9	1.6	13.1
90107	1991	42.6	26.5	22.1	8.8
90123	1991	83.6	3.0	1.5	11.9
90124	1991	67.2	6.0	22.4	4.5
90125	1991	44.4	12.7	17.5	25.4
90129	1991	73.1	17.9	4.5	4.5
90131	1991	85.3	2.9	0.0	11.8
90135	1991	80.6	4.5	10.4	4.5
90138	1991	24.3	47.1	4.3	24.3
90141	1991	90.5	6.3	1.6	1.6
Male					
89025	1989	32.7	11.5	28.8	26.9
89027	1989	11.1	27.8	38.9	22.2
89033	1990	5.4	17.6	50.0	27.0
89034	1990	20.0	7.5	48.8	23.8
89046	1991	22.1	19.1	52.9	5.9
89052	1990	11.5	46.2	32.1	10.3

Table A.3. – continued.

Deer ID	Year[a]	WPR[b]	HPR	TRE	WSA
Male					
89060	1990	33.3	14.7	37.3	14.7
89061	1990	13.0	3.9	59.7	23.4
90078	1990	61.2	10.0	5.0	23.8
90091	1990	14.3	15.6	55.8	14.3
90109	1990	50.7	13.7	16.4	19.2
90128	1991	17.9	43.3	23.9	14.9
90130	1991	28.1	9.4	28.1	34.4

[a] One year of data from each deer was randomly selected for inclusion into habitat selection analyses.

[b] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass.

Table A.4. Hydrologic season home range statistics for radio-collared white-tailed deer included in calibration data set.

Deer ID	Home range size (ha)					Mean distance between consecutive locations (m)				
	89DRY	90WET	90DRY	91WET	91DRY	89DRY	90WET	90DRY	91WET	91DRY
Female										
89002	534	235	190	238	361	846	832	636	577	785
89004	186	184	114	-	-	910	534	563	-	-
89005	154	87	174	125	-	682	520	638	684	-
89008	595	230	203	174	-	1054	720	668	627	-
89014	291	158	140	-	-	911	460	639	-	-
89016[a]	-	-	-	-	-	-	-	-	-	-
89019[a]	-	-	-	-	-	-	-	-	-	-
89021	116	89	77	-	-	371	439	401	-	-
89022	226	185	404	174	-	666	659	1131	836	-
89026	97	94	-	-	-	285	343	-	-	-
89041	213	153	132	239	-	788	518	535	684	-
89045	761	294	331	258	373	919	810	949	760	840
89055	280	184	193	122	-	665	573	569	444	-
89058	262	98	151	182	121	726	396	528	663	724
89059	232	294	-	-	-	910	751	-	-	-
89062	103	96	180	148	-	471	333	494	521	-
89063	107	132	95	184	-	448	499	419	693	-
90067	-	198	381	327	176	-	566	807	713	704
90069	-	512	622	-	-	-	958	1080	-	-

Table A.4. – continued.

Deer ID	Home range size (ha)					Mean distance between consecutive locations (m)				
	89DRY	90WET	90DRY	91WET	91DRY	89DRY	90WET	90DRY	91WET	91DRY
Female										
90081	-	280	737	279	-	-	697	927	1037	-
90107[a]	-	-	-	-	-	-	-	-	-	-
90123	-	-	187	244	266	-	-	614	697	650
90124	-	-	245	167	170	-	-	907	512	741
90125	-	-	158	316	-	-	-	627	679	-
90129	-	-	590	298	589	-	-	920	799	821
90131	-	-	148	170	377	-	-	608	647	608
90135	-	-	433	230	1074	-	-	773	793	1050
90138	-	-	204	295	237	-	-	711	593	569
90141	-	-	656	354	489	-	-	897	704	932
Male										
89003	-	141	297	-	-	-	511	1021	-	-
89017	-	-	77	226	-	-	-	328	706	-
89023	542	268	-	-	-	1859	869	-	-	-
89025	134	221	131	-	-	614	888	651	-	-
89027	106	186	81	186	-	409	774	302	695	-
89033	71	142	55	94	-	315	460	198	435	-
89034	251	302	202	273	208	910	825	667	949	761
89046	184	298	99	283	195	870	973	511	1144	537

Table A.4. – continued.

Deer ID	Home range size (ha)					Mean distance between consecutive locations (m)				
	89DRY	90WET	90DRY	91WET	91DRY	89DRY	90WET	90DRY	91WET	91DRY
Male										
89052	79	359	172	331	203	421	1056	915	1076	1283
89060	114	151	116	134	-	521	440	478	414	-
89061	-	292	270	289	-	-	1212	1121	810	-
90078	-	330	85	341	40	-	1100	437	1195	196
90091	-	191	177	252	-	-	688	599	981	-
90109	-	-	717	922	-	-	-	841	1401	-
90119	-	-	429	323	-	-	-	655	1356	-
90128	-	-	168	892	145	-	-	740	912	758
90130	-	-	88	399	-	-	-	323	654	-

[a] Sufficient data for estimation of summary outcomes for two consecutive seasons were not available.

Table A.5. Mean hydrologic season habitat use (percentage of observations in each habitat) for white-tailed deer included in calibration data set.

Deer ID	Dry season				Wet season			
	WPR[a]	HPR	TRE	WSA	WPR	HPR	TRE	WSA
Female								
89004	41.7	13.9	25.0	19.4	70.3	8.1	10.8	10.8
89005	52.2	4.7	16.4	26.7	56.8	12.2	24.3	6.8
89008	53.0	20.2	14.2	12.6	52.9	23.5	8.8	14.7
89014	33.3	30.8	23.1	12.8	37.6	19.4	22.4	20.7
89022	55.4	0.0	23.8	20.8	65.8	0.0	20.5	13.7
89026	22.5	25.0	40.0	12.5	15.0	42.5	32.5	10.0
89041	16.6	47.5	29.4	6.5	30.6	41.7	27.8	0.0
89045	63.9	16.7	15.3	4.2	46.6	23.2	21.1	9.1
89055	59.0	25.6	11.5	3.8	35.1	40.5	24.3	0.0
89058	40.1	27.2	26.1	6.6	36.6	20.4	26.6	16.4
89059	92.3	2.6	0.0	5.1	83.3	2.8	11.1	2.8
89062	14.7	54.6	16.0	14.7	4.1	65.7	16.5	13.7
89063	32.1	6.4	47.8	13.6	27.3	2.5	55.6	14.7
90067	77.8	11.1	4.9	6.2	67.9	9.3	8.6	14.3
90069	81.1	8.1	8.1	2.7	75.0	5.6	5.6	13.9
90081	86.2	4.1	1.4	8.3	91.7	2.8	2.8	2.8
90123	83.8	0.0	2.7	13.5	73.9	7.0	5.7	13.4
90124	69.4	5.6	25.0	0.0	71.2	5.4	16.1	7.4
90125	41.7	16.7	19.4	22.2	51.4	10.8	21.6	16.2
90129	75.0	16.7	5.6	2.8	75.8	11.4	7.4	5.4
90131	88.9	2.8	0.0	8.3	81.7	2.0	0.0	16.3
90135	77.8	5.6	11.1	5.6	88.2	2.1	7.6	2.1
90138	23.7	60.5	2.6	13.2	27.3	32.7	8.2	31.9
90141	87.5	6.3	3.1	3.1	88.5	4.7	5.4	1.4
Male								
89033	6.8	25.7	41.9	25.7	11.8	21.7	39.7	26.9
89034	10.3	13.3	62.1	14.3	21.8	13.8	35.9	28.4
89046	22.7	20.0	46.8	10.6	21.9	17.4	37.6	23.2
89052	12.9	43.1	33.4	10.6	12.6	48.1	27.7	11.5
89060	45.1	13.1	26.1	15.7	15.1	17.4	50.9	16.6
89061	21.2	12.0	43.1	23.7	9.7	2.8	65.3	22.2

Table A.5. – continued.

Deer ID	Dry season				Wet season			
	WPR	HPR	TRE	WSA	WPR	HPR	TRE	WSA
Male								
90078	57.3	10.1	13.3	19.4	62.2	8.1	10.8	18.9
90091	27.4	12.3	43.8	16.5	3.2	15.6	59.8	21.4
90109	41.2	18.8	22.8	17.2	47.4	18.4	23.7	10.5
90128	27.8	50.0	13.9	8.3	10.6	27.8	39.1	22.5
90130	43.2	8.1	16.2	32.4	11.1	2.8	36.1	50.0

[a] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass.

APPENDIX B
DESCRIPTION OF PARAMETER SYMBOLS USED IN THE CALIBRATION EXPERIMENTS

Symbol	Factor description
ϕ	Maximum affinity for homing beacon
μ	Distance (m) from homing beacon at which affinity is ϕ
λ	Relative affinity for previously visited pixels
ML	Memory length (5-day intervals) for homing beacon and pixel memory
ML_H	Memory length (5-day intervals) for homing beacon
ML_P	Memory length (5-day intervals) for pixel memory
STEP	Number of moves per 5-day interval
$STEP_D$	Number of moves per 5-day interval in the dry season
$STEP_W$	Number of moves per 5-day interval in the wet season
α	Relative affinity for water depths < β cm
β	Water depth (cm) below which relative affinity is α
γ	Water depth (cm) above which relative affinity is 1
A_{WPR}	Relative affinity for wet prairie
A_{HPR}	Relative affinity for herbaceous prairie
A_{TRE}	Relative affinity for tree islands
A_{WSA}	Relative affinity for willow/dense sawgrass
A_{TWS}	Relative affinity for tree islands/willow/dense sawgrass
A_{CYS}	Relative affinity for cypress swamp and prairie
A_{PIN}	Relative affinity for pine
A_{CYP}	Relative affinity for cypress/pine
A_{MAN}	Relative affinity for mangrove
LD_{WEIGHT}	Weight of habitat and water affinity for pixels farther away than one pixel. Weight of habitat and water affinity for neighboring pixels is $1\text{-}LD_{WEIGHT}$.
LD_{PROB}	Probability of habitat and water values farther away than one pixel being included in the movement decision
ML_R	$ML_R \times STEP$ is the length of short term memory (pixels with a relative affinity of $\lambda_R<1.0$)
λ_R	Relative affinity for pixels visited in the past $ML_R \times STEP$ moves

APPENDIX C
SUMMARY OF CALIBRATION EXPERIMENTS FOR FEMALES

Table C.1. Summary of calibration experiment 1 for females.

<table>
<tr><td>Algorithm changes</td><td>Movement algorithms were as described in text (Section 4.2) except that water depth is not included in the movement decision. Habitat accounted for 50% of the movement decision.</td></tr>
<tr><td>Experiment design</td><td>2^{6-1} fractional factorial with 32 EUs, all main effects and first-order interactions were estimable. Simulations were run for 15 years.

Fixed parameters were A_{WPR}=10, A_{HPR}=20, A_{CYP}=A_{PIN}=10, A_{MAN}=1.

<table>
<tr><th>Factor</th><th>Low</th><th>High</th></tr>
<tr><td>ϕ</td><td>3</td><td>5</td></tr>
<tr><td>μ</td><td>750</td><td>1750</td></tr>
<tr><td>λ</td><td>4</td><td>12</td></tr>
<tr><td>STEP</td><td>100</td><td>300</td></tr>
<tr><td>ML</td><td>12</td><td>24</td></tr>
<tr><td>$A_{TRE,WSA}$</td><td>30</td><td>50</td></tr>
</table></td></tr>
<tr><td>Analysis results</td><td>Experimental burn-in was estimated at 4 years, so data from the 5th year of simulation were analyzed.

All average home range sizes were larger than those observed in the field. Discrepancies were significantly smaller with smaller ϕ, smaller μ, larger λ, smaller STEP, and larger $A_{TRE,WSA}$. Distance between consecutive centers ranged from very close to the observed average to more than three times the observed average. Discrepancies were reduced with larger ϕ, smaller μ, and a longer ML. Average distance between consecutive locations ranged from 458 m to 847 m, encompassing the observed value of 686 m. Discrepancies were significantly smaller with smaller μ and larger STEP. On average, simulated deer were observed in tree islands and herbaceous prairie more and wet prairie less than observed deer, indicating a need for further evaluation of habitat relative affinities. An increase in ML and a decrease in STEP caused a decrease in the chi-square discrepancy measure for habitat.

The next experiment will keep current experimental factors the same and add relative affinities for the other habitats.</td></tr>
</table>

Table C.2. Summary of calibration experiment 2 for females.

Algorithm changes	None.
Experiment design	2^{11-6} fractional factorial with 32 EUs, all main effects were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10.

Factor	Low	High
ϕ	3	5
μ	750	1750
λ	4	12
STEP	100	300
ML	12	24
A_{HPR}	20	30
A_{TRE}	20	50
A_{WSA}	30	50
A_{CYS}	5	15
A_{PIN}	5	15
A_{MAN}	1	10

Analysis results	Experimental burn-in was estimated at 5 years, so data from the 6th year of simulation were analyzed. Discrepancies for average home range size were significantly smaller with smaller ϕ, smaller μ, larger λ, smaller STEP, and larger A_{TRE}. Discrepancies for distance between consecutive centers were reduced with larger ϕ, smaller μ, longer ML, and larger STEP. Discrepancies for average distance between consecutive radio-locations were significantly smaller with larger STEP. Discrepancies for habitat use were significantly smaller with smaller A_{HPR}; however, average percent time observed in tree islands was much larger then observed in the field. Mean discrepancy (MD) was significantly reduced with larger ϕ, smaller μ, and longer ML, and larger A_{TRE}. For the subsequent simulation experiment, ϕ was increased, and A_{HPR}, A_{TRE}, and A_{WSA}, and A_{MAN} were reduced. A_{CYS} and A_{PIN} were combined to become A_{CYP} in future experiments.

Table C.3. Summary of calibration experiment 3 for females.

Algorithm changes	None.
Experiment design	2^{10-5} fractional factorial with 32 EUs, all main effects were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10.

Factor	Low	High
ϕ	4	6
μ	750	1750
λ	4	12
STEP	100	300
ML	12	24
A_{HPR}	10	20
A_{TRE}	20	40
A_{WSA}	20	40
A_{CYP}	5	10
A_{MAN}	5	10

Analysis results	Based on experimental burn-in time, year 8 data were analyzed. The largest reduction in mean home range size discrepancy was seen with smaller μ and smaller STEP. Discrepancies for distance between consecutive centers were most reduced with longer ML. Discrepancies for mean distance between consecutive radio-locations were most reduced with larger STEP. Overall, habitat-use patterns were reduced relative to the previous experiment, and discrepancies were most reduced with smaller STEP. MD was reduced with smaller μ and longer ML. For the subsequent simulation experiment, μ was reduced and ML was increased.

Table C.4. Summary of calibration experiment 4 for females.

Algorithm changes	None.
Experiment design	2^{10-5} fractional factorial with 32 EUs, all main effects were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10.
Analysis results	Based on experimental burn-in time, year 8 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ, smaller μ and smaller STEP. Discrepancies for distance between consecutive centers were most reduced with larger STEP and longer ML. Discrepancies for mean distance between consecutive radio-locations were most reduced with larger STEP. Discrepancies in habitat use were most reduced with smaller A_{HPR}. MD was minimized with larger ϕ, smaller μ, larger STEP, and smaller A_{HPR}. For the subsequent simulation experiment, separate memory lengths were used for the homing beacon and the pixel memory algorithms. A_{HPR} was reduced.

Experiment design factors:

Factor	Low	High
ϕ	4	6
μ	500	1000
λ	4	12
STEP	100	300
ML	24	48
A_{HPR}	10	20
A_{TRE}	20	40
A_{WSA}	20	40
A_{CYP}	5	10
A_{MAN}	5	10

Table C.5. Summary of calibration experiment 5 for females.

<table>
<tr><td>Algorithm changes</td><td>The length of the moving window for the homing beacon algorithm and the length of the moving window for the pixel memory algorithm were programmed to be separate parameters the simulation.</td></tr>
<tr><td>Experiment design</td><td>2^{11-6}
estimable. Simulations were run for 15 years.
Fixed parameters were A_{WPR}=10.
<table>
<tr><th>Factor</th><th>Low</th><th>High</th></tr>
<tr><td>ϕ</td><td>4</td><td>6</td></tr>
<tr><td>μ</td><td>500</td><td>1000</td></tr>
<tr><td>λ</td><td>4</td><td>12</td></tr>
<tr><td>STEP</td><td>100</td><td>300</td></tr>
<tr><td>ML_H</td><td>24</td><td>48</td></tr>
<tr><td>ML_P</td><td>6</td><td>36</td></tr>
<tr><td>A_{HPR}</td><td>10</td><td>15</td></tr>
<tr><td>A_{TRE}</td><td>20</td><td>40</td></tr>
<tr><td>A_{WSA}</td><td>20</td><td>40</td></tr>
<tr><td>A_{CYP}</td><td>5</td><td>10</td></tr>
<tr><td>A_{MAN}</td><td>5</td><td>10</td></tr>
</table></td></tr>
<tr><td>Analysis results</td><td>Based on experimental burn-in time, year 8 data were analyzed.
The largest decrease in mean home range size discrepancy was seen with smaller μ and smaller STEP. Discrepancies for distance between consecutive centers were most reduced with larger STEP and longer ML_H. Discrepancies for mean distance between consecutive radio-locations were reduced with larger STEP. Discrepancies in habitat use were reduced most with smaller A_{TRE}. MD was reduced most with larger ϕ, smaller μ, larger STEP, smaller A_{HPR}, and longer ML_H.
For the subsequent simulation experiment, the water depth algorithm was introduced. Also, ϕ, STEP, and ML_H were increased, and A_{TRE} was decreased.</td></tr>
</table>

Table C.6. Summary of calibration experiment 6 for females.

Algorithm changes	The water depth algorithm, as discussed in Section 4.2.2.b. was introduced and weighted as discussed in Section 4.2.2.d.
Experiment design	2^{15-10} fractional factorial with 32 EUs, all main effects were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10.

Factor	Low	High
ϕ	5	7
μ	500	1000
λ	4	12
α	10	30
β	10	30
γ	40	60
STEP	200	400
ML_H	36	60
ML_P	6	36
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	20	40
A_{CYP}	5	10
A_{MAN}	5	10

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with smaller μ, smaller ML_P, and larger λ. Discrepancies for distance between consecutive centers were not affected by any experimental factors and appeared to be nearing zero. Discrepancies for mean distance between consecutive radio-locations were slightly reduced with smaller STEP. Discrepancies in habitat use were most reduced with smaller β. MD was minimized with smaller μ. For the next experiment, μ and ML_P were reduced.

Table C.7. Summary of calibration experiment 7 for females.

Algorithm changes	None.
Experiment design	2^{15-10} fractional factorial with 32 EUs, all main effects were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10.

Factor	Low	High
ϕ	5	7
μ	250	750
λ	4	12
α	10	30
β	10	30
γ	40	60
STEP	200	400
ML_H	36	60
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	20	40
A_{CYP}	5	10
A_{MAN}	5	10

Analysis results	Based on experimental burn-in time, year 8 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ, smaller μ, smaller ML_P, and larger λ. Discrepancies for distance between consecutive centers were reduced with shorter ML_H. Discrepancies for mean distance between consecutive radio-locations were slightly reduced with larger STEP. Discrepancies in habitat use were most reduced with larger A_{WSA} and larger A_{MAN}. MD was minimized with larger A_{WSA}. For the next experiment, A_{WSA} was increased, A_{CYP} was fixed at 7.5, and A_{MAN} was fixed at 10. Simulated deer will make more steps in the dry winter than in the wet summer.

Table C.8. Summary of calibration experiment 8 for females.

Algorithm changes	Individuals moved fewer steps in the wet season than in the dry season by having probability <1 of making a step in each movement iteration.
Experiment design	2^{13-7} fractional factorial with 64 EUs, all main effects and some interactions were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	5	7
μ	250	750
λ	4	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	36	60
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	20	40

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ, smaller μ, smaller ML_P, and larger λ. Discrepancies for distance between consecutive centers were reduced with shorter ML_H. Discrepancies for mean distance between locations were not affected by any experimental factors and appeared to be nearing zero. Discrepancies in habitat use were most reduced with larger A_{TRE}. MD was minimized with smaller μ, shorter ML_H, and larger A_{TRE}. For the next experiment, μ and ML_H were reduced and A_{TRE} was increased.

Table C.9. Summary of calibration experiment 9 for females.

Algorithm changes	None.
Experiment design	2^{13-7} fractional factorial with 64 EUs, all main effects and some interactions were estimable. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	5	7
μ	0	500
λ	4	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	24	48
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	20	40
A_{WSA}	30	50

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ, smaller μ, larger λ and smaller ML_P. Discrepancies for distance between consecutive centers were reduced with longer ML_H. Discrepancies for mean distance between locations were reduced with longer ML_P. Discrepancies in habitat use were not significantly affected by any experimental factors. MD was minimized with smaller μ, larger λ, shorter ML_H, and larger A_{TRE}. Visual assessment indicated that some individuals were still getting 'stranded' in the prairie or getting 'stuck' on a tree island. For the next experiment, an algorithm incorporating habitat and water affinities farther than one pixel from current location was incorporated.

Table C.10. Summary of calibration experiment 10 for females.

Algorithm changes	Introduced algorithm incorporating habitat and water affinities farther then one pixel from current location (Fig. 4.10).
Experiment design	2^{14-9} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	5	7
μ	0	500
λ	4	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	24	48
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	20	40
A_{WSA}	30	50
LD_{WEIGHT}	0.2	0.4

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. Relative to experiment 9 (Table C.9), home range sizes were larger, percent observations in WPR decreased, and percent observations in TRE increased, indicating a shift away from the calibration data. Visual assessment indicated deer were more likely to find and utilize nearby tree islands. The largest reduction in mean home range size discrepancy was seen with larger ϕ, smaller μ, larger λ and smaller ML_P. Discrepancies for distance between consecutive centers were not significantly affected by any experimental factors. Discrepancies for mean distance between locations were reduced with smaller λ and longer ML_P. Discrepancies in habitat use were minimized with smaller A_{TRE}. MD was minimized with larger ϕ. For the next experiment, the habitat and water affinity algorithms were modified further; μ was fixed at 0 m, and several values of several experimental factors (model parameters) were adjusted.

Table C.11. Summary of calibration experiment 11 for females.

Algorithm changes	Probability of habitat and water values farther away than one pixel being included in the movement decision is either 0.5 or 1.0 for each movement step.
Experiment design	2^{14-9} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were μ=0, A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	6	8
λ	6	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	20	28
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	30	40
LD_{WEIGHT}	0.2	0.4
LD_{PROB}	0.5	1.0

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ, larger λ and smaller ML_P. Discrepancies for distance between consecutive centers were significantly reduced with longer ML_H. Discrepancies for mean distance between locations were reduced with longer ML_P. Discrepancies in habitat use were not significantly affected by any experimental factors. MD was minimized with larger STEP. For the next experiment, the homing beacon algorithm was modified.

Table C.12. Summary of calibration experiment 12 for females.

Algorithm changes	Homing beacon algorithm was modified from Fig. 4.7 to Fig. 4.11.
Experiment design	2^{14-9} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were μ=0, A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	6	8
λ	6	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	20	28
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	30	40
LD_{WEIGHT}	0.2	0.4
LD_{PROB}	0.5	1.0

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. Changing the homing beacon algorithm had a large impact on the home range size, as the mean home range area was 111 ha for the simulated deer (compared to means of 271 ha for the observed females and 356 ha for the simulated deer in experiment 11). Any changes in the discrepancy measures due to experimental factors were relatively small. For the next experiment, ϕ was reduced and μ was included as a factor with levels of 0 and 1000 m.

Table C.13. Summary of calibration experiment 13 for females.

Algorithm changes	None.
Experiment design	2^{15-10} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	3	5
μ	0	1000
λ	6	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	20	28
ML_P	3	12
P_{HPR}	10	15
P_{TRE}	15	30
P_{WSA}	30	40
LD_{WEIGHT}	0.2	0.4
LD_{PROB}	0.5	1.0

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger μ. Discrepancies for distance between consecutive centers were significantly reduced with larger μ. Discrepancies for mean distance between locations were reduced with smaller ϕ, larger μ, and longer ML_P. Discrepancies in habitat use were not significantly affected by any experimental factors. MD was minimized with larger μ. For the next experiment, levels of μ were set closer to 1000 m.

Table C.14. Summary of calibration experiment 14 for females.

Algorithm changes	None.
Experiment design	2^{15-10} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10.

Factor	Low	High
ϕ	3	5
μ	750	1250
λ	6	12
α	10	30
β	10	30
γ	40	60
$STEP_D$	400	500
$STEP_W$	$STEP_D$-200	$STEP_D$-100
ML_H	20	28
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	30
A_{WSA}	30	40
LD_{WEIGHT}	0.2	0.4
LD_{PROB}	0.5	1.0

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. Based on the mean outcomes and the discrepancy measures, the current model parameterization appears to be getting close to the ideal on an annual basis, with respect to the calibration data. The largest reduction in mean home range size discrepancy was seen with larger ϕ and smaller μ. Discrepancies for distance between consecutive centers were significantly reduced with larger μ. Discrepancies for mean distance between locations were reduced with smaller ϕ, larger μ, and longer ML_P. Discrepancies in habitat use were most reduced with smaller A_{HPR}. MD also was minimized with smaller A_{HPR}. For the next experiment, several model parameters were held fixed at one value, and other parameter values were adjusted.

Table C.15. Summary of calibration experiment 15 for females.

Algorithm changes	None.
Experiment design	2^{11-6} fractional factorial with 32 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were γ=40, A_{WPR}=10, A_{HPR}=10, A_{WSA}=35, A_{CYP}=7.5, A_{MAN}=10, LD_{PROB}=1.0.

Factor	Low	High
ϕ	2	4
μ	750	1250
λ	10	40
α	10	30
β	10	30
$STEP_D$	400	500
$STEP_W$	$STEP_D$-100	$STEP_D$
ML_H	18	24
ML_P	3	12
A_{TRE}	15	25
LD_{WEIGHT}	0.2	0.4

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ and smaller μ. Discrepancies for distance between consecutive centers were significantly reduced with larger ϕ. Discrepancies for mean distance between locations were not significantly affected by any experimental factors and the mean discrepancy was <100 m. Discrepancies in habitat use not significantly affected by any experimental factors. MD was minimized with larger ϕ. Visual examination of randomly selected movement paths indicated that simulated deer selected the 'best' available habitat (as determined by the relative habitat affinities and water depths) during the small-scale movement step a large percentage of the time. Because it was unlikely that deer would always select the best habitat at all times, the habitat and water depth weights for the second stage of the movement were adjusted in the next experiment. Also, some parameter values were adjusted.

Table C.16. Summary of calibration experiment 16 for females.

Algorithm changes	Probabilities of moving to each 20-m pixel based on habitat and water depth were calculated from relative affinities, and the probabilities of moving to each cell were now calculated as: $$\pi'_j = \frac{1}{4}p'_{1j} + \frac{1}{4}p'_{2j} + \frac{1}{2}\times\frac{1}{9}$$ where p'_{1j} and p'_{2j} were the probabilities of moving to the 20-m pixel j based on habitat and water depth, respectively. The deer selected a 20-m pixel based on a random draw from the multinomial distribution ($\pi'_1, \pi'_2, \pi'_3, \ldots, \pi'_9$).
Experiment design	2^{8-3} fractional factorial with 16 EUs, all main effects were explored. Simulations were run for 15 years. Fixed parameters were μ=1000, λ=30, $STEP_D$=$STEP_W$=400, ML_H=21, A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.2, LD_{PROB}=1.0.

Factor	Low	High
ϕ	2	4
α	10	30
γ	40	60
β	10	30
ML_P	3	12
A_{HPR}	10	15
A_{TRE}	15	25
A_{WSA}	30	40

Analysis results	Based on experimental burn-in time, year 9 data were analyzed. The largest reduction in mean home range size discrepancy was seen with larger ϕ. Discrepancies for distance between consecutive centers were significantly reduced with larger ϕ. Discrepancies for mean distance between locations were reduced with smaller ϕ. Discrepancies in habitat use not significantly affected by any experimental factors. MD was most minimized with larger ϕ. Because the change in the algorithm did not appreciably impact the simulation outcomes, the original weights for 20-m pixel selection were used in future simulations. Future experiments will focus on reducing burn-in time and reducing likelihood of deer moving to a tree island and using it exclusively. Several series of experiments were conducted to develop the algorithm changes in the following experiment (Table C.17) that were not reported in this appendix.

Table C.17. Summary of final calibration experiment for females.

Algorithm changes	To reduce burn-in time for home range size, the homing beacon was 10% of the movement decision at the start of the simulation and was increased to 25% when the simulation reached the length of the memory (as before). Since reducing STEP in the wet season did not produce the desired seasonal changes, this approach was abandoned. Instead, ϕ was decreased by 1.0 if the water depth at P-34 <0 cm (to simulate the deer traveling more to find sufficient forage). To minimize the frequency of deer finding a preferred location and staying there (i.e., staying on a tree island), deer had a very low affinity for pixels visited in the immediate past.
Experiment design	2^3 fractional factorial with 4 replications of each factor combination; all interactions were estimable. Simulations were run for 10 years. Fixed parameters were μ=1000, ϕ=4, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=20, β=10, γ=40, A_{WPR}=10, A_{HPR}=10, A_{WSA}=40, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.2, LD_{PROB}=1.0. Factor / Low / High: STEP: 200, 400 ML_R: 0.2, 0.4 A_{TRE}: 25, 35
Analysis results	Based on experimental burn-in time, year 5 data were analyzed. Home range size discrepancy was reduced with smaller STEP and shorter ML_R. Discrepancies for distance between consecutive centers were significantly reduced with larger STEP. Discrepancies for mean distance between locations were reduced with smaller STEP and shorter ML_R. Discrepancies in habitat use were minimized with larger A_{TRE}. Final model settings were determined based on results from this experiment (see Section 4.4).

APPENDIX D
SUMMARY OF CALIBRATION EXPERIMENTS FOR MALES

Table D.1. Summary of calibration experiment 1 for males.

Algorithm changes	All algorithms were the same as those for the final model for females except the homing beacon. Since males tend to travel more during rut, ϕ was reduced by 1 during rut (July, August, and September) and by ½ just before (June) and just after (October) rut.
Experiment design	2^2 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, ϕ=4, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.2, LD_{PROB}=1.0, ML_R=0.2. Factor / Low / High: STEP: 200, 300 A_{TWS}: 50, 100
Analysis results	Based on experimental burn-in time, year 5 data were analyzed. Home range size discrepancy was reduced with larger A_{TWS}. Discrepancies for distance between consecutive centers were not significantly reduced by either factor. Discrepancies for mean distance between locations were reduced with larger STEP. Discrepancies in habitat use were minimized with larger A_{TWS}. MD was minimized with larger STEP and A_{TWS}. Overall, habitat-use patterns of the simulated males did not correspond well with those observed in the field. The weight of habitat affinity in the movement decision was increased in an attempt to improve habitat use patterns.

Factor	Low	High
STEP	200	300
A_{TWS}	50	100

Table D.2. Summary of calibration experiment 2 for males.

Algorithm changes	Habitat affinity was made to have more impact on the 60-m movement stage by altering the weighted average for calculation of the probability of moving to pixel j (j = 1, 2, 3, . . . , 9): $$\pi_j = 0.35 \times p_{\text{habitat}} + 0.15 \times p_{\text{water}} + 0.25 \times p_{\text{homing beacon}} + 0.25 \times p_{\text{pixel memory}}$$
Experiment design	2^2 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, ϕ=4, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.2, LD_{PROB}=1.0, ML_R=0.2. Factor / Low / High STEP / 200 / 300 A_{TWS} / 50 / 100
Analysis results	Several EUs never reached a steady state (i.e., burn-in not completed). Time plots of the outcome variables indicated percentage of observations in tree islands increased and percentage of observations in wet prairie decreased throughout the 10 year simulation for these runs. No further analyses were performed. In the next experiment, the algorithm change (described above) was reversed, and the weight of the 'long-distance' habitat and water affinities were increased.

Factor	Low	High
STEP	200	300
A_{TWS}	50	100

Table D.3. Summary of calibration experiment 3 for males.

Algorithm changes	Changed weighted average for calculation of the probability of moving to pixel j (j = 1, 2, 3, . . . , 9) back to the original (i.e., four equally weighted factors). Increased ML_R to 0.5.
Experiment design	2^2 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, ϕ=4, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.2, LD_{PROB}=1.0, ML_R=0.5. Factor / Low / High STEP / 200 / 300 A_{TWS} / 50 / 100
Analysis results	Experimental burn-in time was still an issue because four of the sixteen EUs did not reach a steady-state by year 5; however the problem was lessened relative to the previous experiment. Analyses were conducted using year 5 data to indicate a direction for further experimentation. Home range size discrepancy was reduced with larger A_{TWS}. Discrepancies for distance between consecutive centers were not significantly reduced by either factor. Discrepancies for mean distance between locations were reduced with smaller A_{TWS} and larger STEP. Discrepancies in habitat use were minimized with larger A_{TWS}; however, the habitat use of the simulated deer deviated greatly from habitat use of the observed males (i.e., simulated deer were observed more frequently in the prairies and less frequently in the wooded areas than observed males). MD was minimized with larger STEP. LD_{WEIGHT} was increased in the next experiment.

Table D.4. Summary of calibration experiment 4 for males.

Algorithm changes	Increased LD_{WEIGHT} to 0.4 for both the habitat algorithm and the water algorithm for the 60-m stage.
Experiment design	2^2 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, ϕ=4, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.4, LD_{PROB}=1.0, ML_R=0.5. Factor / Low / High STEP / 200 / 300 A_{TWS} / 50 / 100
Analysis results	Simulation burn-in remained an issue because two of the sixteen EUs did not reach a steady-state by year 5; however, year 5 data were analyzed to guide further experimentation with the focus on further optimization of habitat use. With A_{TWS} = 100, habitat-use patterns approached those observed in the field, but simulated deer still were observed more frequently in the prairies and less frequently in the wooded areas than observed males. In the next experiment, ϕ was reduced and several changes were made to the initialization of the simulation.

Factor	Low	High
STEP	200	300
A_{TWS}	50	100

Table D.5. Summary of calibration experiment 5 for males.

Algorithm changes	In previous experiments, starting locations were the same as those used for female experiments. Since observed males were more selective in home range selection, the initialization routine was altered. Starting locations for deer were randomly located within the 1.5 km boundary of the edge of the habitat map. For the first five months of the simulation, the probability of moving to pixel *j* ($j = 1, 2, 3, \ldots, 9$) was calculated as $\pi_j = 0.45 \times p_{\text{habitat}} + 0.45 \times p_{\text{water}} + 0.05 \times p_{\text{homing beacon}} + 0.05 \times p_{\text{pixel memory}}$ After five months, the above probability was calculated using equal weights for all four factors (as in previous simulations). This would allow the deer to have a better opportunity to find suitable home range sites.
Experiment design	2^2 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, ϕ=3, λ=5, λ_R=0.5, ML_H=24, ML_P=6, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.4, LD_{PROB}=1.0, ML_R=0.5. Factor / Low / High STEP / 200 / 300 A_{TWS} / 50 / 100
Analysis results	Based on experimental burn-in time, year 5 data were analyzed. Home range size discrepancy was reduced with larger A_{TWS}. Discrepancies for distance between consecutive centers were not significantly reduced by either factor. Discrepancies for mean distance between locations were reduced with larger STEP. Discrepancies in habitat use were not significantly reduced by either factor. However, the mean percentage of observations in each habitat for the simulated deer was closer to those observed in the field than mean outcomes from the 4th experiment. Within this experiment, large A_{TWS} produced mean percentages of observations in each habitat closer to the observed data. MD was minimized with larger A_{TWS} and larger STEP. STEP was fixed at 250. ϕ and A_{HPR} were included as a factors in the next experiment.

Factor levels (from Experiment design):

Factor	Low	High
STEP	200	300
A_{TWS}	50	100

Table D.6. Summary of calibration experiment 6 for males.

Algorithm changes	None.
Experiment design	2^3 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, λ=5, λ_R=0.5, ML_H=24, ML_P=6, STEP=250, α=10, β=30, γ=60, A_{WPR}=10, A_{HPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.4, LD_{PROB}=1.0, ML_R=0.5. Factor / Low / High ϕ / 3 / 3.5 A_{HPR} / 20 / 40 A_{TWS} / 60 / 90
Analysis results	Based on experimental burn-in time, year 4 data were analyzed. Home range size discrepancies and discrepancies for distance between consecutive centers were reduced with larger ϕ. Discrepancies for mean distance between locations were reduced with smaller ϕ. Discrepancies in habitat use not significantly reduced by any factor. When mean percentages of observations in each habitat for the simulated deer were evaluated, A_{HPR}=20 and A_{TWS}=90 produced outcomes more similar to those observed in the field; however, mean percentage of observations in willow/dense sawgrass (10%) was much lower than expected based on the field data (18%). MD was minimized with larger A_{TWS} and larger STEP. Seasonal shifts also were analyzed. Changes similar to those seen in the field were observed for home range size and distance between consecutive locations, but there was little shift in season habitat use patterns. A_{WSA} was increased relative to A_{TRE}. Algorithm changes to promote seasonal shifts in habitat use were made.

Table D.7. Summary of calibration experiment 7 for males.

Algorithm changes	ϕ was reduced by 1.5 during rut (July, August, and September) and by 0.75 just before (June) and just after (October) rut.
Experiment design	2^3 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were ϕ=3.5, μ=500, λ=5, λ_R=0.5, ML_H=24, ML_P=6, STEP=250, α=10, β=30, γ=60, A_{WPR}=10, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.4, LD_{PROB}=1.0, ML_R=0.5.

Factor	Low	High
A_{HPR}	20	30
A_{TRE}	70	90
A_{WSA}	80	100

Analysis results	Based on experimental burn-in time, year 5 data were analyzed. Home range size discrepancies were reduced with larger A_{TRE}. Discrepancies for distance between consecutive home range centers, mean distance between locations, and habitat use were not significantly reduced by any factor. MD was minimized with larger A_{TRE}. Overall, simulated deer were observed in the wet prairies more and the willow/dense sawgrass less than expected. Seasonal shifts also for home range size and distance between consecutive locations increased relative to the previous experiment, but there was little shift in seasonal habitat-use patterns. Changes in ϕ relative to rut were returned to the levels from the previous experiments (decrease of 1.0 during rut and decrease of 0.5 just before and after run). Weights to calculate the probability of moving to pixel j (j = 1, 2, 3, . . . , 9): $\pi_j = 0.25 \times p_{\text{habitat}} + 0.25 \times p_{\text{water}} + 0.25 \times p_{\text{homing beacon}} + 0.25 \times p_{\text{pixel memory}},$ were adjusted during rut, to reflect decreased use the preferred habitats. Several experiments were conducted to develop the algorithm changes in the final experiment (Table D.8) that were not reported in this appendix.

Table D.8. Summary of final calibration experiment for males.

Algorithm changes	During rut, weights to calculate the probability of moving to pixel j ($j = 1, 2, 3, \ldots, 9$) were $\pi_j = 0.23 \times p_{\text{habitat}} + 0.12 \times p_{\text{water}} + 0.25 \times p_{\text{homing beacon}} + 0.40 \times p_{\text{pixel memory}},$ and the rest of the year weights were $\pi_j = 0.35 \times p_{\text{habitat}} + 0.15 \times p_{\text{water}} + 0.25 \times p_{\text{homing beacon}} + 0.25 \times p_{\text{pixel memory}}.$
Experiment design	2^3 fractional factorial with 4 replications of each factor combination. Simulations were run for 10 years. Fixed parameters were μ=500, λ=5, λ_R=0.5, ML_H=24, ML_P=6, STEP=250, α=10, β=30, γ=60, A_{WPR}=10, A_{TRE}=100, A_{CYP}=7.5, A_{MAN}=10, LD_{WEIGHT}=0.4, LD_{PROB}=1.0, ML_R=0.5. Factor / Low / High: ϕ / 2.5 / 3 A_{HPR} / 25 / 35 A_{WSA} / 100 / 150
Analysis results	Based on experimental burn-in time, year 5 data were analyzed. Discrepancies for home range size distance, between consecutive home range centers, mean distance between locations, and MD were minimized with larger ϕ. Discrepancies for habitat use were minimized with larger A_{HPR}. A_{WSA}=150 produced habitat-use patterns closer to those expected than A_{WSA}=100 did by significantly increasing mean percentage of observations in willow/dense sawgrass. Seasonal shifts in habitat-use patterns were present, but not as large as observed in the field data. Final model settings were determined based on results from this experiment (see section 4.4).

APPENDIX E
VALIDATION DATA SET

Table E.1. Age, residence, and number of radio-locations for radio-collared white-tailed deer included in validation data set.

Deer ID	Capture Date	Age[a]	Residence	Number of observations[b] 1993	1994	Status as of 31 August 1995
Female						
89014R[c]	08 Aug 93	7.5	BCNP	66	75	Censored: 15 Aug 95
90069R	10 Aug 93	6.5	BCNP/ENP	68	-[d]	Dead: undetermined cause (probable stress), 27 Feb 95
90131R	11 Aug 93	5.5	BCNP	66	-	Dead: stress/malnutrition, 29 Oct 94
90135R	09 Aug 93	5.5	BCNP	67	-	Alive/transmitting
93205	26 Jul 93	2.5	BCNP/ENP	67	-	Dead: undetermined cause (probable stress), 03 Mar 95
93206	26 Jul 93	1.5	ENP	67	-	Censored: 22 Nov 94
93208	27 Jul 93	2.5	BCNP	66	75	Alive/transmitting
93210	27 Jul 93	1.5	BCNP	66	-	Dead: stress/malnutrition, 31 Jan 95
93211	28 Jul 93	1.5	BCNP	64	-	Dead: stress/malnutrition,06 Feb 95
93212	28 Jul 93	4.5	BCNP	66	75	Alive/transmitting
93214	02 Aug 93	1.5	BCNP	66	-	Dead: stress/alligator predation, 18 Nov 94
93216	02 Aug 93	1.5	ENP	68	70	Alive/transmitting
93218	02 Aug 93	1.5	ENP	68	69	Alive/transmitting
93219	02 Aug 93	4.5	ENP	68	71	Alive/transmitting
93220	03 Aug 93	2.5	BCNP/ENP	67	-	Dead: undetermined cause (probable stress), 11 Feb 95
93225	03 Aug 93	1.5	BCNP	66	-	Dead: stress/malnutrition, 13 Mar 95
93227	04 Aug 93	2.5	BCNP	66	74	Alive/transmitting
93229	04 Aug 93	3.5	ENP	68	-	Dead: undetermined cause (probable stress), 15 Feb 95
93235	09 Aug 93	1.5	BCNP/ENP	68	-	Dead: undetermined cause (probable stress), 08 Feb 95
93237	10 Aug 93	1.5	BCNP/ENP	68	-	Censored: 30 Apr 95

Table E.1. – continued

Deer ID	Capture Date	Age[a]	Residence	Number of observations[b]		Status as of 31 August 1995
				1993	1994	
Female						
94246	02 Aug 94	1.5	ENP	-	70	Alive/transmitting
94251	02 Aug 94	1.5	BCNP	-	69	Alive/transmitting
94261	02 Aug 94	1.5	ENP	-	69	Alive/transmitting
Male						
89060R	11 Aug 93	7.5	BCNP/ENP	68	-	Dead: undetermined cause (probable stress), 27 Feb 95
91189R	10 Aug 93	3.5	BCNP/ENP	68	-	Dead: stress/alligator predation, 09 Nov 94
93204	26 Jul 93	2.5	ENP	67	-	Dead: undetermined cause, 16 Sep 94
93207	27 Jul 93	2.5	ENP	67	70	Alive/transmitting
93221	03 Aug 93	1.5	BCNP/ENP	67	-	Dead: stress/malnutrition, 12 Mar 95
93226	03 Aug 93	2.5	ENP	56	67	Alive/transmitting
93233	04 Aug 93	1.5	ENP	68	-	Dead: undetermined cause, 04 Dec 94
93234	09 Aug 93	2.5	ENP	68	-	Censored: 14 Feb 95
93236	09 Aug 93	1.5	ENP	68	-	Dead: undetermined cause, 06 Nov 94
94244	01 Aug 94	5.5	ENP	-	70	Alive/transmitting
94247	02 Aug 94	4.5	ENP	-	68	Alive/transmitting
94250	02 Aug 94	2.5	ENP	-	70	Alive/transmitting
94252	03 Aug 94	1.5	ENP	-	71	Alive/transmitting

[a] Age (years) as of date entered into the validation data set.
[b] Annual cycles were 1993 (01 Sep 93 - 31 Aug 94) and 1994 (01 Sep 94 - 31 Aug 95).
[c] R indicates recapture of previously radio-instrumented deer.
[d] Either deer not monitored or <50 observations during the annual cycle.

Table E.2. Annual and hydrologic season home range sizes for white-tailed deer included in the validation data set.

Deer ID	Annual home range (ha)[a]		Seasonal home range (ha)[b]		
	1993	1994	93DRY	94WET	94DRY
Female					
89014R	171	383	149	126	276
90069R	450	-	274	988	-
90131R	769	-	852	244	-
90135R	457	-	421	2138[c]	-
93205	243	-	264	212	-
93206	123	-	118	100	-
93208	128	191	64	163	116
93210	242	-	237	338	-
93211	381	-	293	196	-
93212	1903[c]	428	1518[c]	2420[c]	127
93214	456	-	285	801	-
93216	262	480	245	387	281
93218	145	174	167	151	146
93219	126	85	99	103	50
93220	188	-	185	225	-
93225	347	-	477	230	-
93227	173	509	132	314	338
93229	165	-	161	153	-
93235	269	-	198	654	-
93237	238	-	416	198	72
94246	-	316	-	-	190
94251	-	270	-	-	110
94261	-	325	-	-	232
Male					
89060R	476	-	281	1218[c]	-
91189R	251	-	156	210	-
93204	214	-	107	-	-
93207	261	194	121	266	72
93221	306	-	212	204	-
93226	203	424	238	167	278
93233	135	-	109	111	-
93234	275	-	196	388	-

Table E.2. – continued.

Deer ID	Annual home range (ha)		Seasonal home range (ha)		
	1993	1994	93DRY	94WET	94DRY
Male					
93236	115	-	76	175	-
94244	-	290	-	-	207
94247	-	347	-	-	129
94250	-	349	-	-	176
94252	-	211	-	-	97

[a] Annual cycles were 1993 (01 Sep 93 - 31 Aug 94) and 1994 (01 Sep 94 - 31 Aug 95).
[b] Hydrologic seasons were 93DRY (01 Nov 93 - 30 Apr 94), 94WET (01 May 94 - 31 Oct 94), and 94DRY (01 Nov 94 - 30 Apr 95).
[c] Influential outlier, deleted from summary statistics and analyses.

Table E.3. Mean annual habitat use (percentage of observations in each habitat) for white-tailed deer included in the validation data set.

Deer ID	1993					1994				
	WPR[a]	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS
Female										
89014R	37.9	15.2	36.4	10.6	0.0	46.7	2.7	18.7	13.3	18.7
90069R	72.1	8.8	10.3	8.8	0.0					
90131R	86.4	3.0	6.1	4.5	0.0					
90135R	88.1	1.5	7.5	3.0	0.0					
93205	79.1	7.5	9.0	4.5	0.0					
93206	40.3	16.4	17.9	25.4	0.0					
93208	12.1	16.7	33.3	37.9	0.0	17.3	12.0	57.3	13.3	0.0
93210	71.2	10.6	12.1	6.1	0.0					
93211	32.8	29.7	18.8	14.1	4.7					
93212	95.5	1.5	0.0	3.0	0.0	49.3	8.0	32.0	10.7	0.0
93214	78.8	9.1	3.0	9.1	0.0					
93216	50.0	8.8	29.4	11.8	0.0	61.4	5.7	18.6	14.3	0.0
93218	25.0	48.5	16.2	10.3	0.0	20.3	27.5	46.4	5.8	0.0
93219	13.2	17.6	54.4	14.7	0.0	9.9	14.1	71.8	4.2	0.0
93220	53.7	6.0	32.8	7.5	0.0					
93225	86.4	0.0	7.6	6.1	0.0					
93227	69.7	9.1	10.6	10.6	0.0	33.8	14.9	35.1	16.2	0.0
93229	30.9	51.5	11.8	5.9	0.0					
93235	80.9	4.4	7.4	7.4	0.0					
93237	67.6	7.4	14.7	10.3	0.0					

Table E.3. – continued.

Deer ID	1993					1994				
	WPR[a]	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS
Female										
94246						15.7	52.9	27.1	4.3	0.0
94251						23.2	26.1	39.1	11.6	0.0
94261						23.2	31.9	37.7	7.2	0.0
Male										
89060R	25.0	36.8	29.4	8.8	0.0					
91189R	13.2	5.9	64.7	16.2	0.0					
93204	14.9	1.5	56.7	26.9	0.0					
93207	13.4	13.4	62.7	10.4	0.0	4.3	24.3	62.9	8.6	0.0
93221	44.8	1.5	37.3	16.4	0.0					
93226	16.1	62.5	10.7	10.7	0.0	10.4	47.8	23.9	17.9	0.0
93233	5.9	29.4	55.9	8.8	0.0					
93234	47.1	10.3	26.5	16.2	0.0					
93236	5.9	5.9	76.5	11.8	0.0					
94244						24.3	24.3	27.1	24.3	0.0
94247						16.2	7.4	61.8	14.7	0.0
94250						20.0	17.1	51.4	11.4	0.0
94252						12.7	19.7	64.8	2.8	0.0

[a] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass, CYS = cypress swamp and prairie.

Table E.4. Mean hydrologic season habitat use (percentage of observations in each habitat) for white-tailed deer included in the validation data set.

Deer ID	93DRY					94WET					94DRY				
	WPR[a]	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS
Female															
89014R	41.0	7.7	43.6	7.7	0.0	37.5	18.8	25.0	18.8	0.0	48.7	0.0	10.3	5.1	35.9
90069R	69.2	12.8	12.8	5.1	0.0	72.7	9.1	6.1	12.1	0.0					
90131R	84.6	5.1	7.7	2.6	0.0	80.6	0.0	19.4	0.0	0.0					
90135R	87.2	2.6	7.7	2.6	0.0	75.0	15.6	0.0	3.1	6.2					
93205	76.9	10.3	7.7	5.1	0.0	66.7	15.2	9.1	9.1	0.0					
93206	38.5	17.9	20.5	23.1	0.0	34.4	21.9	28.1	15.6	0.0					
93208	10.3	15.4	33.3	41.0	0.0	31.2	12.5	15.6	40.6	0.0	10.0	10.0	75.0	5.0	0.0
93210	69.2	12.8	7.7	10.3	0.0	87.5	3.1	9.4	0.0	0.0					
93211	28.2	28.2	20.5	17.9	5.1	46.7	23.3	16.7	6.7	6.7					
93212	94.9	2.6	0.0	2.6	0.0	78.1	6.2	15.6	0.0	0.0	25.0	10.0	45.0	20.0	0.0
93214	69.2	12.8	5.1	12.8	0.0	78.1	3.1	15.6	3.1	0.0					
93216	35.9	10.3	35.9	17.9	0.0	59.4	6.2	21.9	12.5	0.0	70.3	0.0	21.6	8.1	0.0
93218	23.1	51.3	17.9	7.7	0.0	28.1	31.2	28.1	12.5	0.0	10.3	23.1	59.0	7.7	0.0
93219	17.9	10.3	59.0	12.8	0.0	9.4	25.0	53.1	12.5	0.0	2.6	10.3	82.1	5.1	0.0
93220	61.5	5.1	33.3	0.0	0.0	65.6	0.0	18.8	15.6	0.0					
93225	84.6	0.0	7.7	7.7	0.0	96.9	3.1	0.0	0.0	0.0					
93227	56.4	12.8	17.9	12.8	0.0	75.0	9.4	6.2	9.4	0.0	8.1	16.2	62.2	13.5	0.0
93229	33.3	51.3	12.8	2.6	0.0	21.9	40.6	34.4	3.1	0.0					
93235	82.1	2.6	7.7	7.7	0.0	71.9	12.5	3.1	12.5	0.0					
93237	71.8	5.1	10.3	12.8	0.0	60.6	21.2	12.1	6.1	0.0	0.0	15.8	71.1	13.2	0.0

Table E.4. – continued.

Deer ID	93DRY					94WET					94DRY				
	WPR[a]	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS	WPR	HPR	TRE	WSA	CYS
Female															
94246											5.3	44.7	47.4	2.6	0.0
94251											10.5	34.2	47.4	7.9	0.0
94261											16.2	21.6	56.8	5.4	0.0
Male															
89060R	12.8	43.6	30.8	12.8	0.0	43.8	21.9	34.4	0.0	0.0					
91189R	10.3	0.0	79.5	10.3	0.0	15.2	15.2	54.5	15.2	0.0					
93204	5.1	0.0	66.7	28.2	0.0										
93207	2.6	15.4	69.2	12.8	0.0	18.8	18.8	53.1	9.4	0.0	0.0	24.3	70.3	5.4	0.0
93221	38.5	0.0	38.5	23.1	0.0	58.1	3.2	16.1	22.6	0.0					
93226	12.5	65.6	9.4	12.5	0.0	16.7	36.7	20.0	26.7	0.0	8.6	48.6	31.4	11.4	0.0
93233	5.1	38.5	48.7	7.7	0.0	9.4	25.0	50.0	15.6	0.0					
93234	35.9	12.8	35.9	15.4	0.0	62.5	9.4	9.4	18.8	0.0					
93236	7.7	7.7	76.9	7.7	0.0	6.2	15.6	62.5	15.6	0.0					
94244											18.4	13.2	42.1	26.3	0.0
94247											10.8	2.7	67.6	18.9	0.0
94250											10.8	21.6	59.5	8.1	0.0
94252											7.7	7.7	84.6	0.0	0.0

[a] WPR = wet prairie; HPR = herbaceous prairie; TRE = tree islands; WSA = willow/dense sawgrass, CYS = cypress swamp and prairie.

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BIOGRAPHICAL SKETCH

Christine Steible Hartless was born on 8 September 1968 in South Bend, Indiana. She received a B.S. in animal science-equine option with a minor in agricultural economics from the University of Kentucky in 1990. While at the University of Kentucky, she worked for the swine nutrition group of the Department of Animal Science in the field, in the lab, and in front of a computer. It was here, doing elementary data analyses, that her interest in statistics was born. She entered the graduate program in the Department of Statistics at the University of Florida in August 1991 and was graduated with a Master of Statistics in May 1993. While working on her master's degree and taking course work towards a Ph.D. in statistics, she worked as a graduate consultant in the statistical consulting lab for the Institute of Food and Agricultural Sciences (IFAS) at the University of Florida. This consulting experience led her to seek a field where she could apply her statistics knowledge to environmental issues. In January 1996, she changed doctoral programs and entered the graduate program in the Department of Wildlife Ecology and Conservation, and she was graduated with a Ph.D. in August 2000.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ronald F. Labisky

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Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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